A CLASSIFICATION OF THE TYRANT FLYCATCHERS (Tyrannidae)

MELVIN A. TRAYLOR JR.[1]

CONTENTS

Abstract. The classification of the Tyrannidae is re-examined, using available morphological, anatomical, behavioral and zoogeographic data. The usual seven subfamilies are reduced to three, and these are defined primarily on cranial characters. The former subfamily Myiarchinae is divided between the Fluvicolinae and Tyranninae, and the remaining "subfamilies" are lumped into one subfamily, the Elaeniinae. Thirty-five genera recognized in the last complete list of flycatchers (Hellmayr, 1927) are synonymized, one is resurrected, and two new ones are recognized, of which one is here described.

INTRODUCTION

This investigation of the classification of the New World flycatchers, Tyrannidae, was undertaken as the first step in the preparation of a list of the family for inclusion in vol. 8 of the continuation of Peters' *Check-list of the Birds of the World* (here usually referred to as "Peters"). The last classification of the whole family was that of Hellmayr (1927), and in the intervening 50 years much that requires assimilation has been learned about the family. David Snow of the British Museum (N.H.) has made similar studies of the Cotingidae and Pipridae, and his results have been published in two recent papers (Snow 1973, 1975).

Before his death in 1957, John T. Zimmer almost completed a manuscript of the Tyrannidae for Peters' *Check-list.* However, Zimmer was concerned almost entirely with species and subspecies, and, with only minor exceptions explained in his earlier published "Studies of Peruvian Birds" (1936–1941), he followed the classification of Hellmayr. While Zimmer's manuscript is invaluable for defining the limits of species and subspecies and their geographical ranges, he had little to say about the genera and higher categories. The present paper deals with those higher categories, and presents the rationale for the classification that will be followed in Peters. A subsequent paper will consider problems at the species level.

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[1] Bird Division, Field Museum of Natural History, Roosevelt Road at Lake Shore Drive, Chicago, IL 60605.

No study of a major family such as the Tyrannidae would be possible without the active assistance and cooperation of one's colleagues. Ernst Mayr, one of the editors of Peters' *Check-list*, first suggested that I edit volume 8, which includes the Tyrannidae, and he has been a source of constant support and encouragement throughout. I have also been fortunate in having Emmet R. Blake as a colleague in residence at Field Museum, with whom I could discuss the innumerable knotty points that arose. In order to examine the genera and species not available in Chicago, I have visited several museums and I would like to thank for their unfailing courtesy: Wesley Lanyon and Lester Short of the American Museum of Natural History, Raymond A. Paynter, Jr. of the Museum of Comparative Zoology, and Frank Gill and James Bond of the Academy of Natural Sciences, Philadelphia. Kenneth Parkes of the Carnegie Museum, Pittsburgh, and George Lowery and John O'Neill of the Museum of Zoology, Louisiana State University, generously lent me necessary material for examination. I was fortunate in having David Snow accept responsibility for the Cotingidae and Pipridae, for we were able to reach complete accord on the limits of our respective families. François Vuilleumier, John Fitzpatrick and John Weske, in both correspondence and personal coversations, have given me the benefit of their field experience with many of the flycatchers, particularly the Andean forms, and W. John Smith has not only done the same, but has given me a copy of his notes on his own flycatcher study. John Fitzpatrick allowed me to see a copy of his manuscript on the genus *Todirostrum* and allies before publication, and has given me permission to reprint one of the figures from the published (1976) version. I have benefited greatly from conversations and correspondence with Allen Phillips, primarily concerning the species of the genus *Tyrannus*. And finally, I am especially grateful to Stuart Warter for permission to freely use his Ph.D. thesis on the classification of the Tyrannoidea—one of the few papers actually defining the Tyrannid subfamilies—and to publish, as Appendix D, some of his figures and tables.

Eugene Eisenmann and John Fitzpatrick were kind enough to critically read the entire manuscript, and to make numerous suggestions for both form and content. I deeply appreciate their efforts to make this a more literate and comprehensive publication. David Snow also read it, to make sure our concepts of the Cotingidae and Tyrannidae were reconciled. I also owe thanks to my wife Marjorie who read the manuscript from the point of view of the intelligent layman and made many helpful suggestions, and to Dianne Maurer who typed it more times than we care to remember.

MATERIALS AND METHODS

External Morphology. During this study I attempted to use evidence from every available source—external morphology, anatomy, behavior and distribution. I personally examined and measured specimens of every genus recognized by Hellmayr, and of those described since the publication of his list. For every genus and for 279 out of 374 ± 1 recognized species, I have plotted the ratios tail/wing, culmen/wing, tarsus/wing and culmen/tarsus as functions of wing length. I selected these ratios as those best suited for comparing the proportions of different sized birds. While wing length is by no means an exact measure of absolute size, it seems the most reliable of the standard measurements.

The different states of various other characters were tabulated for all species. These were: the presence or absence of abnormal primaries, and, if present, in which sex; presence or absence of wing-bars and some measure of their contrast; presence or absence of a dark patch at the base of the secondaries; wing shape, measured by noting the inner primaries to which the 10th and 9th are equal in length, and by calculating the ratio of the wing tip (longest minus shortest primary) to the wing length; type of tarsal scutellation; type of nest; weight by sex; and presence or absence of a bright crest.

Besides the individual characters listed above, the degree of overall resemblance based on plumage color and pattern, general form and size, shape of bill, extent of rictal bristles, etc., is still important in any classification. Such resemblances and differences have been implicit in previous classifications and revisions, even though often subordinated to more artificial key characters. However, convergence in plumage and form is a constant problem, particularly among the smaller, forest-living species, and general resemblance alone is unreliable for diagnoses of genera in this family.

Distribution. The geographic and altitudinal distributions of each genus were plotted on outline maps and tabulated according to the following ecological and geographical divisions:

- I. Lowland humid forest
    - a) Amazonia, including Venezuela and the Guianas
    - b) southeast Brazil
    - c) Colombian-Pacific: the humid forests of Central America, western Colombia and northwestern Ecuador
- II. Other lowland tropical
    - a) woodland/campo/savanna, south of Amazonia
    - b) woodland/llanos, north of Amazonia
    - c) arid: Caribbean coast, Pacific coast of Peru, etc.
- III. Montane forest
- IV. Temperate savanna/puna/paramo
    - a) montane
    - b) lowland Chile and Argentina
- V. Specialized: lacustrine, marshes streams, etc.
- VI. Central America, including tropical Mexico
- VII. North America, including temperate Mexico

Literature. Considering that fifty years have passed since the publication of Hellmayr's list, the literature relevant to the higher classification of the Tyrannidae is surprisingly sparse. Zimmer (1936–1941) discussed in great detail the species of flycatchers occurring in Peru, which include a surprisingly large percentage of those of South America, but his concern was almost entirely with species and subspecies. In his 1955 manuscript, he followed Hellmayr's sequence, although he dropped the subfamilial classification. Zimmer's unpublished list was the basis of Meyer de Schauensee's treatment of the family in his *The species of birds of South America* (1966). In his *A guide to the birds of South America* (1970), Meyer de Schauensee transferred to the Tyrannidae a few genera formerly in the Cotingidae, but otherwise made no changes.

Ames (1971), in his study of the syrinx of passerine birds, examined 128 species in 86 genera of Tyrannidae. He worked within the framework of Hellmayr's classification, that is, he chiefly compared each genus with others in the same subfamily. In his taxonomic conclusions, Ames outlined seven groups of genera (Appendix C) whose members were more closely related to each other than to any genus outside the group, and in some cases he was able to indicate the degree of relationship between the groups. However, he did not attempt to place the groups in a taxonomic hierarchy, and he was left with a residue of thirty-one genera that were neither part of nor allied to any group.

The single paper that directly concerns

itself with the classification of the Tyrannidae as a whole is Stuart L. Warter's (1965) unpublished Ph.D. thesis on the cranial osteology of the Tyrannoidea. Warter examined the skulls of 160 species in 84 genera of the flycatchers. He concluded that cranial characters alone did not support the subdivision of the Tyrannidae into subfamilies, but he combined these characters with the external morphological classification of Hellmayr to produce a tentative classification that differed in several significant ways from Hellmayr's.

A number of authors have dealt with one or the other of Hellmayr's subfamilies, or parts thereof. Meise (1949) reviewed the subfamily Tyranninae, and separated them into three groups of genera primarily on the type of nest. W. John Smith (1966) reviewed the genus *Tyrannus* (including *Muscivora*) primarily from a behavioral point of view, and in 1971 did the same for Hellmayr's Serpophaginae. Smith and François Vuilleumier (1971) reviewed the ground-tyrants, *Ochthoeca*, *Xolmis* (including *Myiotheretes*, *Cnemarchus* and *Ochthodiaeta*), *Neoxolmis*, *Agriornis* and *Muscisaxicola*; in their study Smith emphasized the behavioral characters while Vuilleumier used the morphological and distributional evidence. Most recently, John Fitzpatrick (1976) has reviewed that part of Hellmayr's Euscarthminae including *Todirostrum* and its close allies.

Information on behavior and nest types is scattered through the literature, the one exception being Alexander Skutch's (1960) life histories of Central American birds. Records of weights are even more scattered, although a fair amount of data was gleaned from specimen labels.

The value of the various lines of evidence cited above proved extremely variable when applied to the higher classification of the flycatchers. No single character or group of characters was consistent throughout the family. Proportions—particularly the relative length of the tarsus, which was one of the original characters used in defining subfamilies—vary so much within Hellmayr's subfamilies that they are without value above the generic or generic group level. Such characters as abnormal primaries, bright coronal crests, wing shape, and wing-bars may be regular in some genera or groups of genera, but appear sporadically and irregularly in others.

The type of tarsal scutellation, which was used by both Sclater (1888: 2) and Ridgway (1907: 328 ff.) as a key family character, proves so variable that by itself it cannot even be used to define genera. Only when this scutellation correlates well with other characters can it be said to have taxonomic value. Plotnick and Pergolani de Costa (1955) examined the tarsi of some 12,500 passeriform specimens, and published figures showing that the classical exaspidean, pycnaspidean, taxaspidean and holaspidean tarsal types are not discrete entities, but blend into each other through various intermediate forms.

The importance of the syrinx as a taxonomic character is most difficult to assess. According to Ames (1971: 158), the groups of genera he defines show a high degree of syringeal homogeneity and each possesses certain features not found elsewhere in the family. I believe the homogeneity shown within these groups is real and a true indicator of relationship, because these genera groups correlate well both with the traditional classification and with certain innovations suggested by Warter (1965) on the basis of cranial characters. On the other hand, some genera, which on almost every other character belong in a given group, have syringes that are unlike those of their apparent relatives. *Arundinicola* is not included in the *Fluvicola* group by Ames, even though the two genera are so close that I merge them; *Todirostrum* stands by itself, although *Idioptilon*, with which Short (1975) merges it, is designated by Ames as a member of the *Colopteryx* group; and *Sublegatus*, which is distinguishable from *Elaenia* only by the swollen bill and lack of a white crest, stands completely apart on syrinx from the *Elaenia* group. While close resemblance in the syrinx may be accepted as indicating phylogenetic relationship, the lack of such resemblance apparently does not negate relationship.

The cranial characters used by Warter, the forms of the nasal and interorbital septa, and of the palatines and the cranium, seem to show the greatest consistency in defining taxa above the generic level. These characters not only correlate with each other but with many other characters as well. In only a few cases does the preponderance of evidence from other sources cause me to go against the evidence of the cranial characters. However, the different cranial characters vary in importance from group to group, and no one of them is consistent throughout the family. For example, among the Fluvicolinae and Tyranninae the form of the nasal septum is almost 100 per cent consistent, but among the smaller flycatchers it is quite variable, and the form of the orbital septum is diagnostic.

Methods. Because of the variability shown by all the available criteria, I have not been able to quantify their values in any consistent way. In any given situation, I attempted to use those characters showing the strongest correlations and to ignore single contradictory characters, even though in a different situation the latter might be diagnostic. In other words, my approach has been intuitive, even though I believe it has also been objective. Whether the resulting classification is a valid one can only be determined by time and by many more detailed anatomical studies of the whole family.

In the following discussion I used, for the sake of simplicity, the generic names accepted by Meyer de Schauensee (1966), even though the authors cited have used different ones. I used Meyer de Schauensee's work in preference to Hellmayr's, because the former's names are now in general use and are more familiar to the majority of ornithologists. Appendix B lists all generic names whose status has changed at all since Hellmayr (1927) and names that have been proposed since that date. Use of the appendix should resolve most confusion.

LIMITS OF THE FAMILY

In the most recent widely-used classification of the perching birds, Passeriformes (Wetmore, 1960), the Tyrannidae are a family within the super-family Tyrannoidea, suborder Tyranni, order Passeriformes. They share their superfamily with the New World Cotingidae, Pipridae, Oxyruncidae, and Phytotomidae, and with the Old World Pittidae, Acanthisittidae and Philepittidae. This is also the classification of Mayr and Amadon (1951), except the latter authors use the name "Passeres" for the order, and make the Oxyruncidae a subfamily of the Tyrannidae. Ames (1971: 153), on the evidence of the syrinx, removed the three Old World families to a position "sedis incertae," and placed the Tyrannidae, Cotingidae, Pipridae, Oxyruncidae and Phytotomidae in their own suborder Tyranni. Despite the shifts in higher classification the limits of the latter five families have been remarkably persistent, remaining essentially the same since the mid-nineteenth century.

Mayr and Amadon merged *Oxyruncus* in the Tyrannidae in a parenthetical aside, and did not discuss any characters. Ames (1971: 163) treated the Oxyruncidae as a separate family. He found that *Oxyruncus* had a typically tyrannid syrinx, but no close resemblance to any particular tyrannid genus. The musculature was similar to that of *Pachyramphus* in the Cotingidae, but the cartilages showed substantial differences. Warter was even more positive in keeping *Oxyruncus* out of the Tyrannidae. He stated, "The uniqueness of the highly specialized [*Oxyruncus*] skull argues against the inclusion of the genus in an otherwise so relatively homogeneous a family as the Tyrannidae." I shall follow

Ames and Warter in keeping *Oxyruncus* in a separate family.

Although the families of New World Tyrannoidea have remained essentially the same for the past century, there has been some transference of genera and species between them. In 1907 Ridgway (p. 339) transferred several taxa from the Tyrannidae to the Cotingidae and Formicariidae because they had types of tarsal scutellation other than the exaspidean that he considered characteristic of the Tyrannidae. These genera were *Stigmatura*, *Hapalocercus* (= *Euscarthmus*), *Habrura* (= *Polystictus*), *Muscigralla*, *Culicivora*, *Syristes*, *Idiotriccus* (= *Acrochordopus*), *Elainopsis* (= *Myiopagis gaimardii*), *Tyrannulus*, *Microtriccus* and *Hylonax* (= *Myiarchus validus*). However, Hellmayr recognized, as did Ridgway (1907: 336, ftn.) in another context, that the forms of the tarsal envelope were of dubious value beyond the classification of genera, and sometimes not even there, and he returned (1927) all these genera to the Tyrannidae. Both Warter (1965: 37) and Ames (1971: 162) supported Hellmayr's conclusions.

More recently Ames (1971) and Snow (1973) recommended transferring from the Cotingidae, where they have traditionally resided, to the Tyrannidae the genera *Attila*, *Pseudattila*, *Casiornis*, *Laniocera* and *Rhytipterna*. Ames believed syringeal characters linked these genera into a closely related group, of which the flycatcher genus *Myiarchus* was an integral part. Snow concurred that the five genera did not belong in the Cotingids, although he recognized that so little was known of their behavior, except for *Attila*, it was difficult to reach any conclusions. Warter (1965: 37) also placed *Rhytipterna* in a natural group with *Myiarchus*. However, he considered *Attila*, while definitely not a Cotingid, sufficiently distinct from the other flycatchers as to form a subfamily of its own within the Tyrannidae. Warter did not examine *Casiornis* or *Laniocera*, but he assumed the former was allied to *Attila*, and the latter to *Rhytipterna*. These five genera, based on the then unpublished work of Ames and Warter, were included in the Tyrannidae by Meyer de Schauensee (1970) in his *Guide to the Birds of South America*, and by Wetmore (1972) in his *Birds of the Republic of Panama*; in both cases they were placed next to *Myiarchus*.

Wetmore (1972: 446) also included the Cotingid genus *Lipaugus* in the flycatchers. The genera *Laniocera*, *Rhytipterna* and *Lipaugus* show a remarkable parallelism in the geographical distribution of plumage types. Each genus has a gray species inhabiting Amazonia, and a representative rufous species in Central America and western Colombia. The three genera have always appeared together in linear lists, except for that of Meyer de Schauensee (1970). Snow (1973: 8) remarked on this parallelism, but felt that on behavioral and other plumage characters, *Lipaugus* should be retained in the Cotingas. Ames lacked adequate material of this genus. Warter (1965: 137) found the skulls of *Lipaugus* typically Cotingid, and placed the genus in the subfamily Querulinae. I include *Attila*, *Pseudattila*, *Casiornis*, *Laniocera* and *Rhytipterna* in the Tyrannidae, but leave *Lipaugus* in the Cotingidae.

The final genus added to the Tyrannidae since Hellmayr (1927) is *Corythopis*. *Corythopis* has been considered to form with *Conopophaga* a separate family, Conopophagidae, allied to the Formicariidae and Rhinocryptidae, and included with them in volume 7 of Peters' *Check-list* (1951). Ames, Heimerdinger and Warter (1968) introduced evidence from the sternum, the syrinx, the pterylosis and the antorbital osteology showing *Corythopis* belongs in the Tyrannoidea—not with *Conopophaga*, or with the Formicariids, with which the authors unite *Conopophaga*. Within the superfamily, the syrinx, pterylosis and external appearance are far more typical of the Tyrannidae than of any other family. The authors did not determine the precise relationships of *Corythopis* within the Tyrannids, but the pterylosis resembles that of Hellmayr's Euscarthmines. Meyer de Schauensee (1970: 326) included *Corythopis* in the Tyrannidae, but placed it at the end of the family because he was uncertain of its position. Ames (1971: 67) inserted *Corythopis* between *Euscarthmus* and *Pseudocolopteryx*, but he described the syrinx as "unlike any of the above," meaning the subfamily Euscarthminae.

A difficult genus and species to place is *Xenopsaris albinucha*, which has been transferred back and forth between the Cotingids and Tyrannids several times. The species *albinucha* was originally described in the Cotingid genus *Pachyramphus* (Burmeister, 1869), and was recognized as a Cotingid by Sclater (1893), after he had unaccountably omitted it from his *Catalogue of Birds* (1888). In the meantime, *albinucha* became the type of two new genera, *Xenopsaris* Ridgway, 1891, which the author considered Cotingid and near the genus *Casiornis*, and *Prospoeitus* Cabanis, 1892, which that author considered Tyrannid and near the genus *Serpophaga*. Berlepsch (1907) and Hellmayr (1927) kept *Xenopsaris* in the Tyrannidae, but Zimmer, in his Peters manuscript, removed it to the Cotingids as a subgenus of *Pachyramphus*. Meyer de Schauensee (1966) placed *Xenopsaris* next to *Pachyramphus* but as a separate genus. Finally Smith (1971) tentatively placed it again in the Tyrannidae, in the subfamily Serpophaginae, as did Snow (1973). Unfortunately, neither Ames nor Warter had specimens.

The characters of *Xenopsaris* that most suggest relationship to the Cotingids are its taxaspidean tarsus and the glossy black crown in the male, which is like that of many *Pachyramphus*. Parkes (*in litt.*) considers that its slightly swollen bill with pale cutting edge suggests *Pachyramphus*, and that its sexual dimorphism is similar to that of *Pachyramphus* but has no counterpart among the Serpophagine flycatchers. On the side of Tyrannid relationship, *Xenopsaris* males lack the shortened and pointed 9th primary that is characteristic of males of all *Pachyramphus* species; in size *Xenopsaris* is smaller than any *Pachyramphus*, much nearer the size of the Serpophagines; it builds a cup-shaped nest rather than a large globular structure with side entrance characteristic of the Becards; its vocalizations are unlike those of *Pachyramphus*; and the white outer edge of its outermost rectrix is a common condition in Tyrannids, but not found in *Pachyramphus*. *Xenopsaris*' palustrine habitat would be unique among the Cotingids, but obviously not impossible.

I believe the differences in the 9th primary and in the nest form remove *Xenopsaris* from any close relationship to *Pachyramphus*, and that plumage similarities are, therefore, the result of convergence. This leaves only the taxaspidean tarsus and the bill form and color noted by Parkes *(in litt.)* as characters linking *Xenopsaris* with the Cotingids. While taxaspidean tarsi are characteristic of the Cotingids, they are also found in some Tyrannid genera such as *Culicivora*, *Stigmatura* and *Inezia*. The bill of *Xenopsaris* is more slender than that of *Pachyramphus*, which is the reason Ridgway and Cabanis placed it near *Casiornis* and *Serpophaga* respectively, and the color of the bill is much like that of some species of the Tyrannid genus *Knipolegus*, although unlike any of the Serpophagines. I consider *Xenopsaris* a Tyrannid, but because of the differences in sexual dimorphism and bill color I believe the resemblance to the Serpophagines, particularly to *Serpophaga cinerea*, is due to convergence. Since *Xenopsaris* is of uncertain relationship within the Tyrannids, I shall place it at the end of the family *incertae sedis*.

Warter (1965: 97–100; 138–140) discusses the cranial characters of the Cotingid Tityras [*Tityra* and *Erator*, the latter a genus not recognized by Meyer de Schauensee (1966: 320)] and Becards (*Pachyramphus* and *Platypsaris*). Both groups have essentially Tyranno-Myiarchine skulls, but differ from any of the recognized Tyrannids in a number of characters associated with the nasal capsule. The two *Tityras*, *cayana* and *semifasciata*, are the most aberrant. According to Warter (p. 99), "The peculiar structure of the tityrine bill and nasal capsule . . . provides a character which, by its very uniqueness, constitutes a radical departure from an essentially conservative pattern that obtains throughout the tyrannoid series." The skull of *Erator inquisitor*, however, despite the very close resemblance of that species to *Tityra* in plumage, external morphology, voice and nesting habits, is not so extreme, and shows more resemblance to the Becards. The latter, in turn, seem more closely related to the Tyrannids. Ames (1971: 163) also found that the syringes of the Becards had several Tyrannid features not found in the Cotingas.

Warter (pp. 139–140) suggested a number of alternatives for treating the Tityras and Becards. The first possibility was to emphasize their distinctiveness from the remainder of the Cotingas by recognizing them as a family Tityridae. If further study should show a closer link between the Becards and the Tyrannidae, the former could be made a subfamily, Pachyramphinae of the Tyrannidae, and the separate family Tityridae maintained for *Tityra* and *Erator*. However, he thought the "most logical" action would be to ally the subfamily Tityrinae to the Tyrannidae, recognizing within it two tribes, Tityrini and Pachyramphini. Although I accept his conclusions that the Tityrinae may be closer to the flycatchers than to the Cotingas, I do not consider them the hierarchical equivalent of the other Tyrannid subfamilies that I do recognize, the Elaeniinae, Fluvicolinae and Tyranninae. The skull uniformity among the Tyrannidae of Hellmayr and previous authors does not support the recognition of subfamilies on cranial characters alone (Warter 1965: 131), and the Elaeniinae, Fluvicolinae and Tyranninae are based on a combination of cranial, syringeal, external morphological and behavioral characters. The Tityrinae, however, are tentatively allied to the Tyrannidae only because their crania more nearly resemble those of the Tyrannids than those of the Cotingids. In Peters' *Check-list*, the Tityrinae will be placed at the end of the Tyrannidae, and they will not be considered further in the discussion of subfamilies below.

Two genera of Pipridae have recently been suggested as possible members of the Tyrannidae. Warter (1965: 133) felt that *Neopelma* should properly be in the Tyrannids, and Ames (1971: 160) recommended placing *Piprites* with his *Myiobius* group of Tyrannids. Warter considered *Neopelma* one of several Piprid genera that seemed intermediate between Pipridae and Tyrannidae, and the one most closely resembling the Tyrannids. He did not, however, ally it to any given genus or subfamily. Ames did ally *Piprites* to his *Myiobius* group, including *Myiobius*, *Terenotriccus*, *Pyrrhomyias* and *Onychorhynchus*; this syringeal type was so distinctive that Ames (p. 122) placed his *Myiobius* group in a different structural division from the remainder of the Tyrannidae, along with *Piprites* and the majority of the Cotingas. However, *Piprites*, with its short, deep bill, stout build, short tail and sexual dimorphism, is so unlike any members of his *Myiobius* group, that I think the syrinx resemblance is due to convergence. Unfortunately Ames did not have a specimen of *Neopelma*, nor did Warter have a skull of *Piprites*, so it is not possible to determine if there is a correlation between the syringeal and cranial characters. Snow (1975: 22) recognized that *Piprites* might be related to the Tyrannids, but he preferred to keep it in the piprids for the time being. In view of the uncertainty in both cases, I shall leave *Neopelma* and *Piprites* in the Pipridae, where they are both readily retrievable.

CLASSIFICATION TO SUBFAMILIES

Hellmayr (1927) divided the Tyrannidae into seven subfamilies: Fluvicolinae, Tyranninae, Myiarchinae, Platyrinchinae, Euscarthminae, Serpophaginae and Elaeniinae. Hellmayr did not define his taxa, and before they are critically examined, some attempt must be made to determine what criteria he had in mind. This is not an easy task, nor possibly even a profitable one. As Warter (1965: 130) remarked when discussing family group taxa, "Either the originality of, or the precedent for, the taxa used is often impossible to ascertain." However, a brief history of the development of Hellmayr's subfamilies since Sclater (1888) —the last author to review the whole family and to characterize his subfamilies—may give us some idea of what the former had in mind.

Fluvicolinae – This is the one subfamily that has descended with comparatively little change from Sclater. He characterized it as "Feet strong, tarsi stout, elongated; habits more or less terrestrial; coloration gray, white and black." Morphologically it is extremely heterogeneous, but the species agree in being non-forest types with their center of distribution south of the Amazon and in the temperate zones of the Andes, Argentina and Chile. Ihering (1904: 320) suggested removing *Sayornis* because of its North American distribution, but this was ignored by Berlepsch (1907) and Hellmayr.

Tyranninae – Sclater characterized this subfamily as "Feet strong; tarsi short but strong; habits arboreal but frequenters of more open spaces; coloration olive, gray, white or yellow." Although the name persists, the composition of the family has changed drastically. It originally contained only four of Hellmayr's Tyranninae genera, the remainder of which were in the Elaeniinae, but it also had all the genera of Hellmayr's Myiarchinae. Ihering (1904: 318) recognized a subfamily Pitanginae (Hellmayr's Tyrannine genera *Legatus* through *Pitangus*), which he moved from the Elaeniinae to the vicinity of the Tyranninae, with which they were incorporated by Berlepsch (1907: 473) and Hellmayr (1927). Ihering's reasons for the shift were the wide distribution and aggressive behavior of the Pitanginae. Hellmayr's Tyranninae took final shape when Berlepsch removed those genera now in the Myiarchinae.

Myiarchinae – Set up as a new subfamily by Berlepsch (1907: 476), but nowhere characterized; composed of genera formerly placed by Sclater in the Tyranninae.

Platyrinchinae – Characterized by Sclater as "Feet weak, tarsi thin; forest dwellers; coloration olive and yellow; bill depressed; rictus bristled." Of the 20 genera included by Sclater, only the nominate genus appears in Hellmayr's subfamily! Ihering (1904: 318, 321) dismembered Sclater's family, placing those genera that made a pendent, pyriform nest in a new subfamily, Euscarthminae, and those making a cup-shaped nest in another new subfamily, Serpophaginae. Berlepsch (1907: 482) recognized Ihering's Euscarthminae, although calling it Platyrinchinae, but extracted from it three genera for which he created a new subfamily, Rhynchocyclinae. It was the latter family, to which was added *Platyrinchus*, that became Hellmayr's Platyrinchinae.

Euscarthminae – As noted above, this family was first recognized by Ihering as those genera of Platyrinchinae that made pendent, pyriform nests and were primarily forest forms. It was called Platyrinchinae by Berlepsch and then Euscarthminae again by Hellmayr when he removed *Platyrinchus*. Unfortunately, the name Euscarthminae was there incorrect, because Ihering's type genus *Euscarthmus* was called *Euscarthmornis* by Hellmayr, and he used the name *Euscarthmus* for the taxon known as *Hapalocercus* by Ihering, a cup-nest builder!

Serpophaginae – A family created by Ihering for the genera of Sclater's Platyrinchinae that built open, cup-shaped nests and inhabited open country or the Andes. It was accepted by Berlepsch (he actually called it *subfam. nov.*) and by Hellmayr.

Elaeniinae – The last of Sclater's subfamilies, which he characterized as, "Feet

Table 1.

	Sclater	Ihering	Berlepsch	Hellmayr
Fluvicolinae	"Feet strong; tarsi stout, elongated; habits more or less terrestrial."	suggested removing *Sayornis* to the Tyranninae	as Sclater	as Sclater
Tyranninae	"Feet strong; tarsi short but strong; habits arboreal, but frequenters of more open spaces."	recognized the Pitanginae, Hellmayr's Tyranninae genera *Legatus* through *Pitangus* and placed them near the Tyranninae	incorporated Ihering's Pitanginae; removed the Myiarchinae to a new subfamily	as Berlepsch; only four of Sclater's 17 genera remain
Myiarchinae	(in the Tyranninae)	(in the Tyranninae)	created a new subfamily, but nowhere diagnosed it	as Berlepsch
Platyrinchinae	"Feet weak; tarsi thin; forest dwellers; bill depressed; rictus bristled."	divided it into two new subfamilies—Euscarthminae making pendent, pyriform nests, and Serpophaginae making cup-shaped nests	Ihering's Euscarthminae; created a separate subfamily Rhynchocyclinae for *Rhynchocyclus*, *Tolmomyias* and *Ramphotrigon*	Berlepsch's Rhynchocyclinae plus *Platyrinchus*, the oldest name. Only the nominate genus remains from the 20 included by Sclater
Euscarthminae	(genera in Platyrinchinae)	created for those genera of Sclater's Platyrinchinae making pendent, pyriform nests; also included *Rhynchocyclus* from the Elaeniinae	(called Platyrinchinae)	called Euscarthminae, but Hellmayr's genus *Euscarthmus* was actually Ihering's *Hapalocercus*, a cup-shaped nest builder
Serpophaginae	(genera in Platyrinchinae)	created for those genera of Sclater's Platyrinchinae making a cup-shaped nest	as Ihering	as Ihering
Elaeniinae	"Feet weak; tarsi thin; forest dwellers; bill compressed; rictus smooth	removed the Pitanginae, Hellmayr's Tyranninae from *Legatus* through *Pitangus*, to near the Tyranninae; removed *Rhynchocyclus* to the Euscarthminae	as Ihering	as Ihering

weak; tarsi thin; forest dwellers; coloration olive and yellow; bill compressed; rictus smooth." After Ihering (1904: 318) removed the Pitanginae—"large birds with strong bills that biologically much approximate to true Tyranninae"—and *Rhynchocyclus*, because of its pendent nest, the subfamily was accepted unchanged by Berlepsch and Hellmayr.

These changes are summarized in Table I.

The families of Sclater, except for the Fluvicolinae, have been so strongly revised that his original characters are no longer pertinent. Even Sclater's characters for the Fluvicolinae are irrelevant, for such genera as *Muscipipra* have among the shortest tarsi in the family instead of "stout, elongated." The Myiarchinae were never defined, and it is hard to know what Berlepsch had in mind, because they vary from some of the larger *Myiarchus*, with wings 90–100 mm to *Terenotriccus* with wing 52 mm, and from the small, round winged, forest haunting *Myiobius*, to the large, open-country, pointed winged *Hirundinea*. Ihering's separation of the Euscarthminae from the Serpophaginae on the basis of nest type was a major advance, because this character correlated well with proportions of bill and tarsi, but there were, and still are, so many problem genera for which the nest type is unknown, that its usefulness is limited.

Certainly mensural characters do not in any way define the present subfamilies. Taking wing length as a criterion of size, all the Tyranninae are larger than any of the Euscarthminae and Serpophaginae; otherwise there is overlap among all the subfamilies. The same is true of proportions. A species with a wing 62 mm, tail 52 mm, culmen 14 mm and tarsus 18 mm would fit in any subfamily except the Tyranninae without distorting the present limits of the taxon. It is clear that the present subfamilies are based on such qualitative characters as the form of the bill, the extent of the rictal bristles, the shape of the wing and tail, habitat, distribution, color and pattern. This does not imply that such a classification is valueless; Sclater, Ihering, Berlepsch and Hellmayr were all highly capable and experienced ornithologists, and the classification they developed improved at each stage. However, it is futile to search their work for key mensural or morphological characters that would clearly define their subfamilies.

In the literature since Hellmayr, there have been no attempts to evaluate his subfamilies. Ames (1971) used the subfamilies of Hellmayr as the framework within which he conducted his investigation of the syrinx. His genus-to-genus comparisons were almost all intra-subfamily, and although he set up groups of related genera, he expressly avoided equating them with subfamilies. Zimmer (1936–1941) in his *Studies of Peruvian Birds*, and also in his preliminary manuscript for Peters, ignored subfamilies. He could hardly have studied the Peruvian flycatchers, which include over half the known species, without forming some ideas about subfamilies. However, no hint of them appears in his works, and he followed the order of genera in Hellmayr's list without change. In one instance one gets the impression that he doubted the reality of some of the subfamilies completely. When he (1940b: 19) transferred *Mecocerculus superciliosus* and *Leptopogon nigrifrons* to the genus *Phylloscartes*, he merely stated "there are no positively distinguishing characters between these two species and various species of *Phylloscartes*," and he did not mention the fact that the genera had been assigned by Hellmayr to three different subfamilies, Serpophaginae, Elaeniinae and Euscarthminae respectively.

The one study that discusses the Tyrannidae at the subfamily level is that of Warter (1965). Although his cranial characters alone did not support the separation of the Tyrannidae into subfamilies they did, when combined with the classification of Hellmayr based on biological and external morphological characters, suggest a revised classification that Warter (p. 131) presented "merely as a model for other workers."

In his study of the Tyrannoidea, Warter used five cranial characters:

a) nasal septum – six forms of the nasal septum were recognized (only five occurred in the Tyrannidae), which were determined by the type of supporting structure and by the presence and form of the transverse plate.

b) interorbital septum – five states of the interorbital septum were recognized (only four in the Tyrannids), characterized by the number and extent of the fenestrae.

c) prepalatines – three states, determined by their flattening and curvature.

d) cranium – three forms of the cranium depending on overall configuration.

e) palatomaxillaries – presence or absense recorded.

In his Figures 2 and 3 (Appendix D), Warter illustrates the states of his cranial characters.

Warter examined the crania of 850 specimens of flycatcher, representing 160 species in 84 genera. In his Table II (Appendix D) he lists the state of each of his five characters by genus. The Tyrannidae as a whole are homogeneous and there were too few long series to adequately investigate individual variation at species level; therefore his treatment had to be at the genus or group of genera level (p. 93). This problem did not exist among the more heterogeneous Cotingas, where single skulls of the genera and even some of the species, may be readily identified. In his Table II, Warter lists the genera in the order of Hellmayr.

Warter's Table II as reprinted here (Appendix D) differs slightly from the form in which it appeared in his dissertation. With his permission, I have included several ambiguous entries from an earlier draft that were eliminated from the final copy. These additions have been enclosed in parentheses; figures outside the parentheses, including the question marks, are those of his final version. The ambiguities are consequent upon the difficulty of assigning characters to a given type because of 1) shot damage, 2) careless cleaning, 3) overly zealous dermestids or 4) a continuum of form requiring arbitrary assignment to one type or the other. These ambiguous states are included here to help evaluate which data are equivocal, and which relatively certain.

When Warter's characters are compared with Hellmayr's classification, there is a strong correlation between the individual character states, and sometimes complexes of states, and the broad groupings of genera. This inspires confidence that both the evolved classification of Hellmayr and Warter's cranial characters reflect real relationships among the Tyrannidae, and not just superficial resemblance or convergence. The most striking example is found in the Tyranninae, all species of which have a character complex including type 1 or 2 nasal septum without basal plate, and types 1 interorbital septum, palatines and cranium. It is highly improbable that such a complex of four characters would have evolved independently more than once, thus the Tyranninae are almost certainly a monophyletic group. Since the cranial characters do correlate so well overall with what is known of Tyrannid relationships, they should be given considerable weight when they diverge from the old classification.

Warter (p. 94) found that the three subfamilies of "larger" flycatchers, Fluvicolinae, Tyranninae and Myiarchinae, lent themselves better to characterization than the four remaining subfamilies of "smaller" flycatchers. Although, as noted before, there is overlap in size among almost all subfamilies, the latter four of Hellmayr—Platyrinchinae, Euscarthminae, Serpophaginae, and Elaeniinae—have a preponderance of small species, for which skeletal material is less common, and, being delicate, are frequently damaged. Warter (p. 96) stated, "Perhaps largely as a result of insufficient material, the adequate characterization of the smaller flycatchers, is, at the present time, impossible."

Within the larger flycatchers, there is a clear dichotomy. The Tyranninae of Hellmayr are a distinct group as outlined above. Belonging to this group, as shown by identical cranial characters, are the genera *Myiarchus* and *Eribates* of Hellmayr's Myiarchinae, and *Rhytipterna*, placed by Hellmayr and his predecessors in the Cotingidae. Presumably part of the same complex, although Warter had no material of them, are *Hylonax*, which has been synonymized with *Myiarchus* by Lanyon (1967b: 339); *Deltarhynchus*, which is a *Myiarchus* with a short broad bill; and *Laniocera*, which has been considered a close relative of *Rhytipterna* except by Ridgway (1907), who placed it in the Pipridae while leaving *Rhytipterna* in the Cotingidae. The second group of large flycatchers is composed of the Fluvicolinae of Hellmayr and most of the remaining genera of that author's Myiarchinae, the genera *Nuttallornis* through *Myiophobus*. This group is characterized by a type 6 nasal septum with horizontal baseplate, and either types 2 or 3 of at least two of the remaining three characters; the type 2 interorbital septum occurs almost exclusively in this group, although types 1 and 3 occur as well. Warter (p. 95) considers that the second group's two subgroups, the Fluvicolinae and the remainder of the Myiarchinae respectively, may be distinct on characters too minor to justify separation at the subfamily level. They merge insensibly together through such genera as *Ochthoeca*, *Ochthornis* and *Entotriccus* and may represent terrestrial or semi-terrestrial and arboreal divisions of the same stock.

A third group that Warter (pp. 95, 140) feels should be attached to the section of large flycatchers, either as a subfamily or "subfamily-equivalent" group are *Attila* and the probably closely related *Pseudattila* and *Casiornis*, two genera not available to him. Skulls of *Attila* were essentially Tyranno-Myiarchine, but with the following differences: interorbital septum less completely ossified (type 5, not found elsewhere in the Tyrannidae); nasal septum incomplete, shallow, along its entire length; prepalatines narrow, slightly convergent, nearly straight. In themselves, the *Attila* skulls were a distinct type. Warter's suggestion was to recognize among the large tyrant flycatchers three "subfamily-equivalent" groups: Attilinae, Tyranninae and Fluvicolinae.

Warter, as noted before, did not consider that cranial characters permitted the classification of Hellmayr's four subfamilies of small flycatchers at this time. He did believe (p. 131) the Euscarthminae graded into the Platyrinchinae via *Todirostrum* and *Oncostoma*, and the Serpophaginae graded into the Elaeniinae via *Serpophaga*. He also included in this section the genus *Onychorynchus*, which, like *Platyrinchus*, has a type 3 nasal septum and does not belong in either section of the Myiarchinae, the subfamily where Hellmayr placed it.

Warter's (p. 131) final tentative classification of the Tyrannidae was a compromise between the cranial evidence and the subdivisions of Hellmayr based on biological and external morphological features. It included five subfamilies, three of them divided into tribes:

- Attilinae (see Warter, pp. 95 and 140)
- Tyranninae
- Fluvicolinae
    - Fluvicolini
    - Alectrurini
    - "Contopini"
- Platyrinchinae
    - Onychorhynchini
    - Platyrinchini
    - Euscarthmini
- Elaeniinae
    - Elaeniini
    - Serpophagini

The classification adopted in this paper is essentially that of Warter at the subfamily level, except that I do not recognize his Attilinae, and I consider that all of the small flycatchers, his Platyrinchinae and Elaeniinae, belong in a single subfamily for which Elaeniinae is the oldest name. The use of tribes, however, does not seem warranted. The three Fluvicoline tribes are uneven, both in numbers of genera and degree of difference, and the Fluvicolini and "Contopini" may not be so distinct as previous classifications would suggest. The tribes of Elaeniinae, which Warter recognized in deference to previous classifications, seem to merge into each other so insensibly that no divisions can be recognized.

The brief history of the evolution of Hellmayr's subfamilies showed that none of them was maintained on clear-cut characters, and that the Myiarchinae had never been diagnosed, not even by the original describer. The dismemberment of the Myiarchinae, therefore, may upset our sense of familiarity with a subfamily of 70 years' standing, but it does not do violence to any known diagnostic characters. The more important question is how well do the segments of Myiarchinae fit into the Tyranninae and Fluvicolinae respectively.

Myiarchus, with the closely related *Eribates*, *Hylonax* and *Deltarhynchus*, fits easily into the Tyranninae. It is a highly successful genus, like so many of those in the Tyranninae, with a geographical range equal to that of *Tyrannus* itself, from temperate North America to temperate South America. Form and proportions are typically "flycatcher," with a long, broad and moderately flattened bill and about average development of rictal bristles. The tarsi are longer than those of most of the Tyranninae, but still short enough that Sclater put them in with the "tarsus short, stout" Tyranninae. The hole nesting habits of *Myiarchus* are shared for the most part with *Myiodynastes*. There are no evident reasons for keeping *Myiarchus* out of the Tyranninae, and the cranial evidence for placing it there is compelling. The latter statement is also true for *Rhytipterna* and presumably *Laniocera*, and the transfer of these two genera to the vicinity of *Myiarchus* on other grounds by Snow (1973) and Ames (1971) reinforces the cranial evidence. Meyer de Schauensee (1970) and Wetmore (1972) followed Ames and Warter, whose theses they had seen before publication.

The recognition of Warter's subfamily Attilinae, *Attila* and *Casiornis*, must be considered here, because the above authors all included those genera, previously included in the Cotingidae, with *Rhytipterna* and *Laniocera* next to *Myiarchus*. Externally, there is nothing that keeps *Attila* and *Casiornis* separate from *Rhytipterna*, *Laniocera* or *Myiarchus*. Internally, there is strong evidence from the syrinx that they are closely related. The above five genera make up Ames' (1971: 160) *Myiarchus* group. Speaking of the former Cotingid genera compared to *Myiarchus*, Ames says, "Without assuming interdependence of several syringeal features, it is difficult to see how two groups of birds could evolve both external and internal similarities to such a degree." If this is true when *Attila*, *Casiornis*, *Laniocera* and *Rhytipterna* are compared to *Myiarchus*, it is equally true when *Attila* is compared to *Rhytipterna* and the others. Despite the fact that *Attila* has a partially ossified interorbital septum not found elsewhere in the Tyrannidae, which caused Warter to put it in a separate subfamily, I consider Ames' *Myiarchus* group to be monophyletic, and I keep it together in the Tyranninae.

The transfer of the remainder of the Myiarchinae, Warter's "Contopini," to the Fluvicolinae suggests some relationships not considered before. Both are presumably old lineages with a high degree of sympatry in the larger genera, numerous monotypic genera and relict species, and a high degree of phenetic variability. Warter's Fluvicolini contains all the truly terrestrial flycatchers and is usually thought of as a long-legged group. However, there are a number of arboreal Fluvicolines, such as *Ochthoeca* and *Knipolegus*, and these are very close in proportions to the Contopines. When the two are treated as related, certain cases of resemblance between genera and species that were previously thought of as convergence may turn out to show close relationship. A striking example is the Fluvicoline *Ochthoeca diadema* and the Contopine *Myiophobus flavicans*. Both are bright olive green flycatchers, identical in wing length and shape, bill form, and rictal bristles; they can be separated only by the slightly longer tarsus and yellow superciliaries of *diadema*, and the yellow crest of *flavicans*. Their resemblance may be due to the persistance of the characters of an early common ancestor.

The Fluvicolines of Sclater and Hellmayr are a heterogeneous assemblage united by their dry country or temperate center of distribution in South America. Their great phyletic age has produced such unlike forms as the long-legged, long-billed terrestrial *Muscisaxicola* and the short-legged, short-billed arboreal *Muscipipra*. It is encouraging, and a tribute to Sclater's intuition, that Warter's cranial characters support the present classification. Warter's Contopines on the other hand, are a lineage that has had its most successful radiation in North and Central America. While there was a proliferation of species in the Fluvicoline genera *Muscisaxicola*, *Agriornis* and *Xolmis* in the south temperate and subtropical regions, there was a similar proliferation in the Contopine *Contopus*, *Empidonax* and *Sayornis* in the north temperate regions and Middle America. The Fluvicolines are still virtually all South American, with only one species reaching eastern Panama, while only a few genera of Contopines are primarily South American. These are mostly small, lowland forms, such as *Myiobius* and *Terenotriccus*, or montane forest genera such as *Myiotriccus*, *Pyrrhomyias* and *Myiophobus*. These South American genera may have separated from the North and Central American group fairly early, because some at least have a distinctive type of syrinx, as discussed below. However, in general form all these genera are fairly close, being "typical" small flycatchers with broad, depressed bills and moderate to heavy rictal bristles.

Three of Ames' genera groups are included in the expanded Fluvicolinae. The first of these, his *Fluvicola* group, belongs to what might be called the core of Warter's Fluvicolini: *Xolmis*, *Neoxolmis*, *Agriornis*, *Muscisaxicola*, *Fluvicola*, *Gubernetes*, *Knipolegus*, *Muscipipra* and *Phaeotriccus*. With the possible exception of *Gubernetes* and *Muscipipra*, one would expect these genera to be alike. What is surprising is the absence of *Arundinicola*, *Entotriccus* and *Yetapa*, which are in all morphological characters except the syrinx very close to *Fluvicola*, *Phaeotriccus* and *Gubernetes* respectively. Ames' second group is the *Nuttallornis* group—*Nuttallornis*, *Sayornis*, *Contopus*, *Blacicus*, *Empidonax*, *Aechmolophus*, and *Aphanotriccus*—which according to Ames is closest to the *Fluvicola* group in syringeal structure. It is this group that has been so successful in North and Central America.

The members of Ames' *Myiobius* group —*Myiobius*, *Terenotriccus*, *Pyrrhomyias* and *Onychorhynchus*—appear more closely related to each other than to any other group, and Ames placed them in a separate major structural division of the syrinx from the rest of the flycatchers. This is the group that is primarily of South American forest distribution. The inclusion of *Onychorhynchus* with the *Myiobius* group agrees with the traditional classification of Hellmayr, but differs from that of Warter, who considered the genus an aberrant "small" flycatcher in his subfamily Platyrinchinae. The status of *Onychorhynchus* is considered in more detail below.

The remainder of the family, which Warter, in deference to previous classifications, divided into two subfamilies and five tribes, seems to me incapable of such subdivision.

Consider first the cranial characters. The nasal septum, which has proved an important conservative character in the Fluvicolinae and Tyranninae, is extremely variable in the Elaeniinae, and lacks any correlation with other characters. On the other hand, his tribes Platyrinchini, Euscarthmini and Serpophagini, and some genera of the Elaeniini, all show a type 4 interorbital septum, which does not occur at all in the large flycatchers. Of those Elaeniini genera that lack the type 4 interorbital septum and that might be set apart on that account, three are linked to the Serpophagini by their type 5 nasal septum, which is unique to these two groups. As Warter said (p. 112) characterization of the smaller flycatchers on the basis of their cranial characters is impossible.

The external morphological and biological evidence for subdividing the small flycatchers is little better, despite the four subfamilies usually recognized. *Onychorhynchus*, with its striking ornamental crest, long, flat bill, and long rictal bristles, is out of place in any group; it fits no better with the small flycatchers than with the Myiarchinae, where Hellmayr placed it. It is seemingly related to *Platyrinchus* by the type 3 nasal septum, which is found only in these two genera, but *Platyrinchus* has a short, broad, flattened bill, a modest concealed crest, and makes a simple cup-shaped nest rather than the elaborate, pendent, pyriform nest of *Onychorhynchus*. *Platyrinchus* is somewhat out of place in its own tribe because of its peculiar nasal septum and simple cup-shaped nest. Warter (p. 131) found that on cranial characters the Platyrinchini and Euscarthmini intergraded through *Todirostrum* and *Oncostoma*, and that the Serpophagini and Elaeniini were related through *Serpophaga*. On external morphological and biological characters I can find no way to characterize family-level groups. There are certain core groups that are quite distinct, such as the flat-billed *Rhynchocyclus* type, the tody-flycatchers *Todirostrum* and allies, and the small-billed generalized *Elaenia* group, but there are more genera falling between these groups than within them.

Ames' two genera groups from this part of the family are essentially two of these core groups. His *Colopteryx* group—*Colopteryx*, *Oncostoma*, *Idioptilon*, *Hemitriccus*, *Myiornis* and *Lophotriccus*—are all members of what I call *Todirostrum* and allies, although *Todirostrum* itself has a distinctive syrinx and is not placed with the others. His *Elaenia* group includes *Elaenia*, *Suiriri*, *Camptostoma*, *Tyrannulus* and *Phaeomyias*, all part of what I call the small-billed generalized *Elaenia* group. However, the *Rhynchocyclus* type, that I mention as a core group, is considered by Ames as an artifact of convergence. Speaking of *Platyrinchus*, *Tolmomyias* and *Rhynchocyclus*, he (p. 161) says that they, "differ so strongly in their syringeal structure that one may seriously question the reliability of bill shape as a common character for the five genera" [including *Cnipodectes* and *Ramphotrigon*, which he had not seen]. Ames' evidence agrees with that of the nasal septum and nesting habits to show that *Platyrinchus* is out of place even in the restricted subfamily where Hellmayr put it.

The recognition of any Elaeniinae subdivisions, either the earlier subfamilies or Warter's tribes, would give a sense of certainty about the reality of these entities that is non-existent.

The sequence of subfamilies and of genera in the family lists for Peters' *Check-list* ideally go from primitive or generalized to advanced or specialized. Historically, the lineal list of the flycatchers has begun with the Fluvicolinae, and ended with the Tyranninae (Sclater, 1888) or the Elaeniinae (Berlepsch, 1907; Hellmayr 1927). Although there is little solid evidence, the flycatchers seem most nearly related to the Pipridae, with Elaeniine flycatchers and the sexually monomorphic Piprids nearest the ancestral line. Warter

(p. 111) found the skulls of the Piprids *Tyranneutes* and *Neopelma* flycatcher-like, and intermediate between the flycatchers and typical Piprids. This suggested an intermediate position for the Pipridae between the Cotingidae and Tyrannidae. Ihering (1904: 319) came to a similar conclusion many years before when he considered that the Pipridae and Tyrannidae descended from a common ancestor whose closest relatives were among the Elaeniinae (*sensu stricto*) in the Tyrannids and the Ptilochlorinae (including *Tyranneutes* and *Neopelma*) in the Piprids. The ancestral form was presumably small, olive green, arboreal and forest-living, with a short, somewhat compressed and bristled bill; a description that fits many genera among the Elaeniinae. Ames (1971: 150) did not find syringeal characters useful taxonomically in determining relationships among the higher categories of Tyrannoidea. As he says (p. 157), "Except for the *Piprites-Myiobius* complex and *Ilicura*, the few manakins examined show little syringeal similarity to the typical members of either the Tyrannidae or Cotingidae."

Assuming that the Elaeniine flycatchers are the most generalized or primitive, then the Fluvicolinae, with their many terrestrial forms, are the most specialized, and the Tyranninae are the most "advanced." I use "advanced" in the sense of most successful and presumably most recently evolved, for not only are the genera widely spread geographically, from North America or Mexico to southern South America, but many individual species are equally widespread. Fitzpatrick (*in litt.*) points out that wide distributions in the Tyranninae are almost always associated with open country and edge habitats, and bear no relation to recent speciation. However, the extreme uniformity in cranial characters among the Tyranninae, and the similarity in external morphology among them compared to the diversity in the Fluvicolinae, suggest to me a more recent proliferation. The sequence of the subfamilies for Peters' *Check-list* will therefore be: Elaeniinae
Fluvicolinae
Tyranninae

SEQUENCE AND RELATIONS OF GENERA

The sequence of genera that follows (Appendix A) relies heavily on tradition when there is no strong evidence to suggest a change. If I had started *de novo*, I might well have made considerable changes. However, they would have been based on characters no more conclusive than those of Berlepsch or Hellmayr. There being no advantage in producing a new sequence just for the sake of change, much of the following list follows Hellmayr, but in reverse.

ELAENIINAE

Just as the subfamilies were placed in the sequence of primitive or generalized to advanced or specialized, so should the genera be within a subfamily. While the concepts of primitive and advanced are difficult to apply with confidence to many of the flycatcher taxa, it should be possible to recognize certain groups as generalized or specialized. If we accept the concept of the manakins and flycatchers as evolving from a common stem, then some of the small green flycatchers of the restricted subfamily Elaeniinae are probably closest to the ancestral stock. They are generally olive green above, with the crown sometimes gray or dusky; paler below, whitish, yellow or olive; two pale wing-bars and pale edgings on remiges; bill short and constricted, and light rictal bristles. Genera that fall naturally into this group are *Xanthomyias*, *Phyllomyias*, *Tyranniscus*, *Oreotriccus* and *Acrochordopus*. They have almost certainly diverged some from the common primitive stock between manakins and flycatchers, because that was presumably a humid forest form as are many of the manakins today, and the above genera are found in drier, woodland habitats or in the subtropical zone. They are, however, unspecialized, at least morphologically.

The characters used to define the above genera are minor. *Phyllomyias* has a broader, more triangular bill and heavier rictal bristles than *Xanthomyias*; *Oreotriccus* is considered to have an exaspidean tarsus while the others are pycnaspidean or "quasi-exaspidean"; *Tyranniscus* has a short, compressed bill; *Acrochordopus* has the most pointed wing and a pycnaspidean tarsus with the distal scutella roughened; *Oreotriccus* has a rounded wing. Plumage patterns, however, cut directly across the generic lines. *Acrochordopus burmeisteri*, *Phyllomyias fasciatus*, and *Xanthomyias virescens* are virtually identical in plumage; they can only be distinguished by the morphological characters listed above; the same is true of the pairs *Oreotriccus plumbeiceps* and *Tyranniscus cinereiceps*, and *Xanthomyias sclateri* and *Phyllomyias* (*Oreotriccus*) *griseocapilla*. The last named species, *griseocapilla*, was transferred from *Phyllomyias* to *Oreotriccus* by Zimmer (1955: 23) because of its exaspidean tarsus. However, *Phyllomyias fasciatus* shows individual variation from exaspidean to taxaspidean (Zimmer called it pycnaspidean, but with birds this size the tarsal types are difficult to distinguish), and the tarsal scutellation is not a valid generic character. With the exception of a group of species now in *Tyranniscus* that I separate below, I unite in one genus *Xanthomyias*, *Phyllomyias*, *Tyranniscus* (*nigrocapillus*, *uropygialis*, and *cinereiceps* only), *Oreotriccus* and *Acrochordopus*. *Phyllomyias* and *Tyranniscus* are equally available (both described by Cabanis and Heine, 1859: 57) as the oldest name; I select *Phyllomyias* since I split the present genus *Tyranniscus*, and the use of that name might cause confusion.

Zimmer (1955: 24) pointed out that the species of *Tyranniscus* fall into two groups on wing pattern. The species *nigrocapillus* (type of genus), *uropygialis* and *cinereiceps* have the common wing pattern of two wing-bars, pale edgings on the flight feathers, and a contrasting black patch at the base of the secondaries. The remaining species, *vilissimus*, *bolivianus*, *cinereocapillus*, *gracilipes* and *viridiflavus*, have a pattern unique among the tyrannids. The median and greater coverts are edged along the outer webs with yellow or white, rather than having the pale coloring at the tips producing a wing-bar; the secondaries and four or five subexternal primaries are edged with yellow, but the outermost and the four or five inner primaries are black. This produces a distinctive black stripe (wedge) down the wing when it is spread. Correlated with this type of wing is a longer bill and a much less accentuated black speculum on the secondaries. Zimmer believed both types had quasipycnaspidean tarsi, but in my notes on the tarsi, made before I was aware of the plumage types, I called *nigrocapillus*, *uropygialis* and *cinereiceps* "pycnaspidean/taxaspidean" and *vilissimus*, *bolivianus*, *cinereocapillus*, *gracilipes* and *viridiflavus* "exaspidean, some pycnaspidean proximally." Ames (1971: 162) noted a distinction in the syrinx. He found *nigrocapillus* like *Ornithion*, and *chrysops* (a race of *viridiflavus*) like nothing else. His comment (p. 162) was, "The two species of *Tyranniscus* examined differ so strikingly in syringeal morphology that I felt it necessary to verify the identity of the specimens through comparison with skins. One cannot help wondering if a thorough analysis of structural and behavioral characters of these and other species of *Tyranniscus* would not result in dividing the genus." Warter (1965: 157) examined specimens of *Tyranniscus acer* (a race of *gracilipes*), *chrysops* and *vilissimus*. They had the type 6 nasal septum, otherwise found only in the Fluvicolinae and the aberrant *Polystictus*. *Xanthomyias virescens*, the only other member of my *Phyllomyias* group that he examined, had a type 1 nasal septum, also found in several other genera of the enlarged Elaeniinae.

Published behavioral data on *Tyranniscus* are virtually non-existent. However, John Weske (*in litt.*) says *nigrocapillus* forages like a kinglet, but *bolivianus* perches and sallies like a typical flycatcher. Distributionally the three barred-wing forms, *nigrocapillus et al.*, are all Andean subtropical; the "edged" forms are divided, *vilissimus* occurring in Central America, and Caribbean Colombia and Venezuela, and *gracilipes* in Amazonia, while *bolivianus*, *cinereicapillus* and *viridiflavus* are found in the Andean subtropics, sympatric with the *nigrocapillus* group. In the Vilcabamba Range in Peru, Weske (*in litt.*) found the range of the edged-winged *bolivianus* overlapped those of the two barred-winged species *nigrocapillus* and *uropygialis*, while the last two replaced each other altitudinally without overlap. Only two nests have been recorded—Snethlage (1935: 538) reported the nest of *acer*, a race of *gracilipes*, as large, triangular, retort-shaped and hung from the tree branches at middle height, and Skutch (1960: 465) described that of *vilissimus* as a cozy ovoid structure with a side doorway, found in hanging mosses or bromeliads. Unfortunately, *acer* and *vilissimus* have the same wing type and there is no comparative material of *nigrocapillus et al. Phyllomyias griseocapilla* and *burmeisteri*, however, both build cup-shaped nests.

Despite the superficial similarity, I believe the group of *Tyranniscus* species with the unique wing pattern, syrinx and aberrant nasal septum, should be separated generically from the typical group of species. Surprisingly, there is no name available, so I propose:

Zimmerius gen. nov., type *Tyrannulus chrysops* Sclater, 1858.

Diagnosis. Superficially most like *Tyranniscus* Cabanis and Heine, 1859, but differs as follows: has a unique wing pattern in which the median and greater coverts, the secondaries and four or five subexternal primaries are edged with yellow, while the outermost and four or five internal primaries are blackish, producing a black wedge when the wing is spread; tail proportionately longer, greater than 80 per cent of wing length instead of less than 80 per cent, and bill proportionately longer, greater than 18 per cent of wing length; tarsus basically exaspidean with a few scutes on the proximal half of the plantar surface, compared to taxaspidean/pycnaspidean in *Tyranniscus*; syrinx unlike any others in the Elaeniinae, lacking intrinsic muscles; nasal septum of Warter's (1965: 34) type 6 with transverse plate, a type found elsewhere only in the Fluvicolinae and in the unrelated *Polystictus* of the Elaeniinae. When *Tyranniscus* is merged with *Phyllomyias* (incl. *Xanthomyias* and *Oreotriccus*) the wing pattern, syrinx and nasal septum of *Zimmerius* remain as diagnostic characters, but the different proportions and tarsal envelopes are covered by variation in *Phyllomyias*.

The species included in *Zimmerius*, all formerly in *Tyranniscus*, are *bolivianus*, *vilissimus*, *cinereicapillus*, *gracilipes* and *viridiflavus* (including *chrysops*). The genus is named for the late John Todd Zimmer in belated recognition of his enormous contribution to the systematics of Neotropical birds, and his recognition of the unique wing pattern in this new genus.

Although I have *Zimmerius* follow *Phyllomyias* in the lineal list, I am not convinced they are closely related. There is, however, no other genus to which they seem more nearly related, so leaving them together will at least retain the benefit of familiarity.

Ornithion (including *Microtriccus*) is a genus of quite small flycatchers with disproportionately short tails. In plumage pattern, *O. inerme* is not unlike *Phyllomyias* (*Tyranniscus*) *nigrocapillus*, but much smaller; the other two species lack any wing-bars. *Ornithion inerme* is intermediate in tail length between "*Microtriccus*" *brunneicapillum* and *semiflavus* and the shortest tailed *Phyllomyias* in its size range. The values of the tail wing ratios are: *brunneicapillum* and *semiflavus*, 54 per cent and

57 per cent; *inerme*, 70 per cent; and *P. griseiceps*, 87 per cent respectively. The tarsi are taxaspidean/pycnaspidean, but the tarsi are so variable in this whole Elaeniine group of flycatchers, that they are not good indicators of relationship. Ames found the syrinx of *semiflavus* to be near *P. nigrocapillus* and probably related to *Elaenia*. In cranial characters *Ornithion* seems typical of many small flycatchers. Although there are no really trenchant characters to diagnose *Ornithion*, the included species are a cohesive group, and I recognize it.

Tyrannulus elatus is a small genus and species, similar to the smaller *Zimmerius* in size and proportions, but nearer *Phyllomyias nigrocapillus* in plumage pattern. It has generally been included with these genera in lineal lists, but it differs from both of the above in having a partially concealed bright yellow crest. Bright crests are common in the flycatchers, and have undoubtedly arisen independently in a number of different lineages. However, they are not known to occur in only one species of an otherwise crestless genus, and I do not think that *elatus* belongs in either *Phyllomyias* or *Zimmerius*. On the other hand, *elatus* is almost a miniature of *Myiopagis gaimardii*, and I believe that is where its relationships lie. Both genera have taxaspidean tarsi, and Ames (1971: 161) included *Tyrannulus* and *Myiopagis* in his *Elaenia* group on syringeal characters. Warter (1965: 34), however, found that *T. elatus* and *M. gaimardii* (which he included in *Elaenia*) differed in their types of nasal septum, interorbital septum and cranium. The relationship of *elatus* with *M. viridicata* was closer, but both skulls were damaged, so that the evidence was inconclusive. *Tyrannulus* should be placed next to but not in *Myiopagis*.

Camptostoma, *Phaeomyias*, *Sublegatus*, *Suiriri*, *Myiopagis* and *Elaenia* are a group of closely related genera. They are more successful than the genera previously discussed in the sense that all except *Suiriri* are found throughout the tropical lowlands of South America, and three reach Mexico or the southwestern United States. With the exception of *Sublegatus*, all are included in Ames' *Elaenia* group on syringeal characters.

Phaeomyias is basically a monotypic genus for the type, *murina*, but Hellmayr and Zimmer added or subtracted other species. Hellmayr (1927: 453) included *tenuirostris*, a species that Zimmer (1955: 2) properly removed to *Inezia*. Prior to that, Zimmer (1941b: 10) added *Elaenia leucospodia* because of its partially taxaspidean tarsus. The latter character, however, is of little value by itself; in some species, such as *Phyllomyias fasciatus*, the tarsi can vary from taxaspidean to exaspidean with every gradation in between. *Leucospodia* has a partially concealed white crest, similar to those of *Elaenia* or *Myiopagis*, and should not be placed in a crestless genus without more substantial evidence. Actually, in every available character of size, proportions, pattern and nest-type, *leucospodia* is a typical *Myiopagis*; the only difference is that all *Myiopagis* have at least some yellow or olive in their plumage (as does *Phaeomyias murina*), while *leucospodia* is plain dull brown, whitish below. This latter coloration is not unusual in species endemic to the arid coast of Peru, and I place *leucospodia* in *Myiopagis*.

Phaeomyias murina is about as "typical" a dull brownish flycatcher with yellowish belly as one could visualize; its only distinctive external character is a fairly broad, whitish superciliary. *Camptostoma* is a smaller version of the same, but with a compressed, arched bill. Both are members of Ames' *Elaenia* group, along with *Suiriri*, *Myiopagis* and *Elaenia*, but *Phaeomyias* and *Camptostoma* have type 2 nasal septa, without the transverse plate, while *Suiriri* and *Elaenia* have type 5 with plate. The situation in *Myiopagis* is uncertain, with *gaimardii* having type 5, *viridicata* probably type 1, and the others not examined.

Camptostoma and *Phaeomyias* agree in general form and color, and in all syringeal and most cranial characters; however, they differ strongly in voice and behavior according to both Eisenmann and Fitzpatrick (*in litt.*). One of the most marked differences between them is in the form of their nests. *Camptostoma* builds a globular nest with a side entrance, placed in branches of low trees, while *Phaeomyias* builds a neat cup, typical of the *Elaenia* group of genera. Ihering considered the nest of *Camptostoma* transitional between the cup-shaped nest of his Elaeniinae and Serpophaginae, and the pendant nest of his Euscarthminae. However, *Camptostoma* itself shows no relation to the Euscarthmines, being a typical member of the *Elaenia* group in color, form and syringeal characters. Despite its close resemblance to *Phaeomyias*, I keep it separate because of the differences in behavior and nest form.

The genus *Sublegatus* is composed of three parapatric species (to be discussed in a separate paper) found throughout practically all of lowland South America, although probably not resident in the rain forest. It differs from most *Elaenia* only in the lack of a white crest, and its somewhat swollen bill with wholly black mandible; it can be told from *E. cristata* only by the bill characters. It builds a shallow cup-shaped nest like *Elaenia*, and Warter (1965: 34) records them as having similar, but not identical, crania. In fact, there is little besides intuition that leads me to keep *Sublegatus* out of *Elaenia*, and the fact that the three species of *Sublegatus* form a different speciation pattern from that of any *Elaenia*.

Suiriri is composed of two hybridizing taxa, which Zimmer (1955: 18) thought should be treated as a single species, but which Short (1975: 283), presumably working with the same material, maintains as two species. They differ from *Elaenia* in lacking a white crest, and in having a longer bill with solid black mandible. The eastern species *affinis* differs from any *Elaenia* in having the rump and proximal quarter of the rectrices pale yellow in contrast to the olive back and blackish tail; however, it differs from the congeneric (possibly conspecific) *suiriri* in the same way. The most distinctive character shown by *Suiriri* is the white spotting of the juvenal plumage. All the grayish-brown dorsal feathers of the juvenal plumage have a wedge-shaped white tip, as do the wing coverts and three inner secondaries. When viewed from above, the juvenal bird shows a startling resemblance to juvenal Old World flycatchers of the genus *Muscicapa*; the pattern is unique in the Tyrannidae, except that juvenal *Sublegatus* has white spotting on the crown, according to Fitzpatrick (*in litt.*).

Although *Myiopagis* has always been associated with *Elaenia*, and many authors have followed Hellmayr (1927: 401) in uniting the two, Zimmer (1941a: 20) considered them distinct genera. He kept them separate because of the pycnaspidean or taxaspidean tarsus of *Myiopagis*, and the usually yellow (white in some subspecies of *gaimardii*) rather than the usually white crown in *Elaenia*. Ames found the syrinxes alike, but Warter (1965: 37) recorded *M. viridicata* (the type of the genus) as having a type 2 nasal septum, while *gaimardii* had a type 5 like *Elaenia*. As pointed out by Eisenmann (*in litt.*), *Elaenia* species prefer open habitats where they are relatively conspicuous, and *Myiopagis* species prefer denser foliage where they are relatively inconspicuous. I recognize *Myiopagis*, but with the knowledge that further anatomical research may suggest either merging it with *Elaenia*, or transferring species between them.

Elaenia is the largest and most "successful" of the Elaeniine genera, with 19 species occurring from southern Mexico to Tierra del Fuego, and from both humid and arid lowlands to above 3000 meters in the Andes. Although there is no single character by which to diagnose the genus, it is a natural assemblage whose limits are generally accepted. In size, the species range from medium to large for this group of genera, wings 70 mm to 91 mm, with relatively short bills, 16–18 per cent of wing except for *cristata* in which it is 20 per cent and short to medium tarsi, 20–26 per cent of wing. The bill is short, moderately broad at the base and deep throughout, rictus lightly bristled, and wing usually fairly pointed, 10th primary equal to 4th to 6th. Plumage is generally dull olive above, except for males of *strepera*, which are dark slate gray, and the underparts are pale yellowish to olive to whitish; the majority of species have a concealed white crest. As far as recorded, all species build a neat cup-shaped nest, frequently covered with lichens.

The genera thus far discussed make up Warter's tribe Elaeniini, with the exception of *Leptopogon*, *Mionectes* and *Pipromorpha*, which will be inserted in the lineal list further on. The adjoining tribe of Warter, the Serpophagini, I consider to merge into the Elaeniini without the slightest break. *Serpophaga* and *Myiopagis* have been confused in the past, *M. caniceps* having been described in both genera, and as recently as 1957 Dorst described a population of *Myiopagis gaimardii* as *Serpophaga berliozi* (see Mayr, 1971: 313). *Mecocerculus* is also an obvious bridge. *Mecocerculus* species are remarkably close in plumage to *Phyllomyias* species. Intergeneric pairs showing especially close resemblance are *M. hellmayri* and *P. uropygialis*, *M. minor* and *P. plumbeiceps*, and *M. poecilocercus* and *P. sclateri*. The only plumage character that consistently distinguishes *Mecocerculus* is the distinct white superciliary. On the other hand, Ames (1971: 73, 74) found the syrinx of *Mecocerculus* like that of *Serpophaga* and *Anairetes*. Smith (1971: 285), on the basis of his behavioral studies of Hellmayr's Serpophaginae, considered *Mecocerculus* closely related to *Serpophaga* (incl. *Inezia*), *Anairetes* (incl. *Uromyias*) and *Stigmatura*. Finally Warter (1965: 34) recorded *Mecocerculus* as having a type 5 nasal septum, which it shared only with *Elaenia* and its closest relatives, and with *Serpophaga*, *Inezia*, and *Anairetes*. There seems little question that the former subfamilies or tribes were artifacts.

The genus *Inezia* is similar to *Serpophaga* in size, proportions and general plumage pattern. Hellmayr's *Inezia* consisted only of the species *subflava*, but Zimmer (1955: 1) added to it *Serpophaga inornata* and *Phaeomyias tenuirostris*. Smith (1971: 266) included *Inezia* in *Serpophaga* because of similarities in appearance and behavior. However, Parkes (1973: 249) has pointed out that the *Inezia* species differ from *Serpophaga* in lacking a white crest, and in having taxaspidean instead of exaspidean tarsi, pale instead of black mandibles, and a distinctive juvenal plumage rather than one like the adult plumage. I consider this combination of characters sufficient to define the two genera. There is also a close resemblance in plumage between *Inezia subflava* and the two species of *Stigmatura*. The latter are characterized by greater size, proportionately long tails and a nasal septum without a basal plate. The relative tail lengths compared to wing lengths of *Stigmatura budytoides* and *napensis* are 121 per cent and 113 per cent respectively, compared to 98 per cent in *subflava*. The plumage pattern of the three species is basically the same, upperparts olive brown, with a prominent white or pale yellow superciliary stripe running to well behind the eye; underparts pale yellowish; two distinct white wing-bars, and flight feathers edged white. The tails of both are rounded, but those of *budytoides* and *napensis* are elaborately patterned with white, while that of *subflava* is only narrowly tipped. Although the resemblance is close, I recognize *Inezia* and *Stigmatura* as distinct genera, primarily because of the difference in nasal septa, the former having a type 5 and the latter a type 2.

Anairetes, *Uromyias* and *Yanacea* are a closely related group of genera. They are composed of long-tailed, long-legged species, found in the upper subtropical and temperate zones of the Andes and south through Chile and Patagonia to Tierra del Fuego. *Yanacea alpinus* and *Uromyias agraphia* are practically unstreaked, recalling *Stigmatura*, but *Uromyias agilis* is heavily streaked on throat and breast, similar to *Anairetes* species. *Uromyias* was separated from *Anairetes* because of its long tail with pointed rectrices, and *Yanacea* was recognized because of its relatively shorter bill and tarsus. These characters do not seem of great importance in an otherwise closely related group, and I merge *Yanacea* and *Uromyias* in *Anairetes*. Zimmer (*Ms.*) had already merged *Yanacea* and *Anairetes*, as he suggested in an earlier discussion (1940b: 10); Smith (1971: 275) merged *Uromyias* and *Anairetes*.

Tachuris, the brilliantly colored *Siete Colores*, has regularly been associated with *Serpophaga*. Smith (1971: 284) says it probably belongs with the Serpophagines, but it may have closer relatives in the Euscarthmines. He did not specify which of the latter, but possibly it is near *Pseudocolopteryx*, which also has marsh-living forms. However, the color and patterning of *Tachuris* are unique, particularly the blue auriculars, and there is no way to relate it closely to any of the other smaller flycatchers. The combination of orbital septum, palatines and cranial type are found throughout the Elaeniinae, and the nasal septum was undetermined (Warter 1965: 34); Ames found the syrinx unlike any other. I shall leave *Tachuris* in the vicinity of *Serpophaga*, but it could equally well be *sedis incertae*.

Colorhamphus parvirostris was placed in the genus *Ochthoeca* by Berlepsch (1907: 470), but was kept in its monotypic genus near *Serpophaga* by Ridgway (1907: 396) and Hellmayr (1927: 400). I agree with Berlepsch, and discuss *parvirostris* in more detail under *Ochthoeca*.

Culicivora, *Polystictus*, *Pseudocolopteryx* and *Euscarthmus* have been kept at the end of the Euscarthminae since Berlepsch (1907). The subfamily Euscarthminae was created by Ihering (1904) for a group of genera making pendant, pyriform nests, and its type genus *Euscarthmus* had at that time for its type species *Euscarthmus nidipendulus* Wied, a species now in the genus *Idioptilon*. *Culicivora* and allies show no particular resemblance to the typical *Todirostrum/Idioptilon* group, and are in some ways nearer *Serpophaga*. All but *Euscarthmus* have one or more species with whitish or streaked crests as in *Serpophaga*, they all have weak rictal bristles, and all make cup-shaped nests. In bill length they are intermediate between the long-billed *Todirostrum* and the shorter-billed Serpophagas. They seem to form a natural group, with their center of distribution in the dryer country of southeastern Brazil and northern Argentina and, except for *Culicivora*, with isolated populations in dry country north of the Amazonian forest. *Pseudocolopteryx* has penetrated the more temperate zones in Patagonia and the southern Andes, and three of the four species are sympatric in the Chaco. The four genera seem worth recognizing. *Culicivora* has a most peculiar rounded tail, with only 10 rectrices, and the barbs are stiff and decomposed, recalling *Synallaxis* in the Furnariidae. *Polystictus* has an aberrant cranium, with nasal septum, interorbital septum and palatines characteristic of *Fluvicola* rather than the Elaeniinae. *Pseudocolopteryx* is a natural assemblage of predominantly yellow species with marked sympatry among them, suggesting a long phylogenetic history; three of the four species have aberrant primaries. The two species of *Euscarthmus* are rich browns and buffs with rufous crests; they have frequently been allied to *Pseudocolopteryx*, but I hesitate to unite them because the latter is so uniform without *Euscarthmus*.

Leptopogon, *Mionectes* and *Pipromorpha* were placed at the end of the restricted Elaeniinae by Berlepsch (1907: 492). *Pipromorpha* had been merged in *Mionectes* for many years until Ridgway (1907: 354)

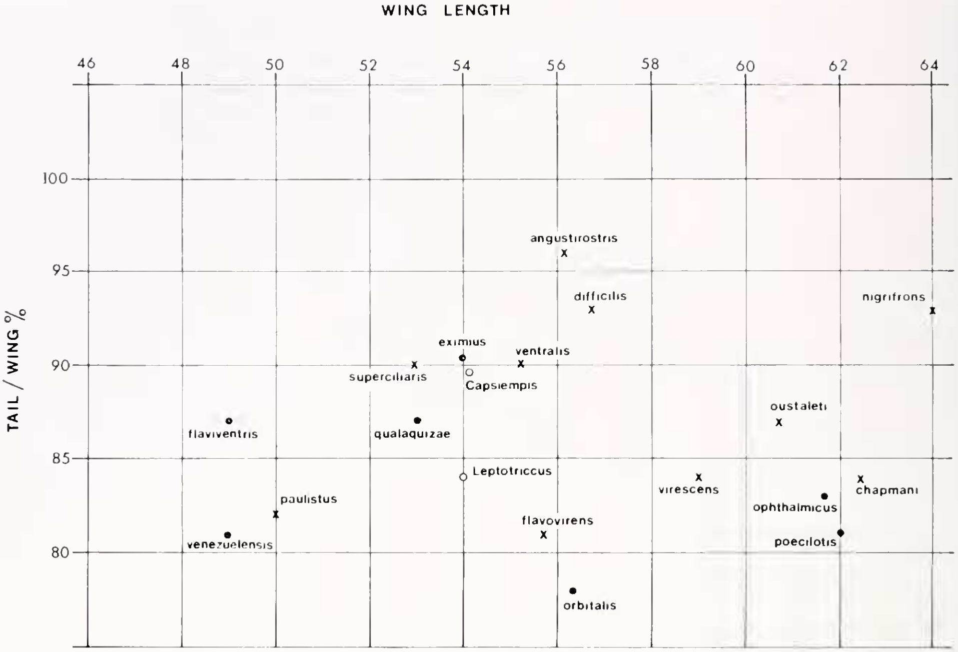

Figure 1. Proportions of tail/wing plotted as functions of wing length for species of the genera *Phylloscartes*, *Pogonotriccus*, *Leptotriccus* and *Capsiempis*. Although these genera were originally separated because of differing proportions, the points fall into a continuum. Closed circles, "●", are *Pogonotriccus*, crosses, "×", are *Phylloscartes*, and open circles, "○", are the types of the monotypic genera *Leptotriccus* and *Capsiempis*.

resurrected it because of the different shapes of the 9th primaries in adult males. This is a trivial character in a family where, in a single genus such as *Pseudocolopteryx*, three species have different sets of primaries aberrant, and the fourth has them all normal. In all other morphological and anatomical characters—size and proportions, bill shape and lack of rictal bristles, syrinx and cranial characters—*Pipromorpha* and *Mionectes* are virtually identical, and I again merge them. *Leptopogon* is close to *Mionectes* in size and proportions except for its longer tail, and both genera make pendent, globular nests, usually hung under logs or cut banks in the vicinity of water; this is unlike the nests of any Elaeniine flycatcher. According to Monroe (1975), they also share the behavioral trait, unusual among the Tyrannids, of single-wing flicking. Besides the peculiar nest, *Leptopogon* differs from the Elaeniine group in having fairly heavy rictal bristles, but this character is not shared with *Mionectes*. *Leptopogon* differs from *Mionectes* in having a much more rounded wing, longer tail, heavier rictal bristles, and normally shaped primaries; in all *Mionectes* species but *rufiventris*, males have either the 9th or 10th primary notched, shortened or attenuated. According to published accounts, there seems to be little difference in behavior.

The section of the subfamily where *Leptopogon* and *Mionectes* seem most at home is with *Phylloscartes*, *Pogonotriccus* and allies. In plumage and pattern, *Leptopogon* is particularly close to *Phylloscartes* and *Pogonotriccus*, in fact four of the species in the latter genera were originally described in *Leptopogon*. Superficially, there is little difference between *Leptopogon* and *Phyl-*

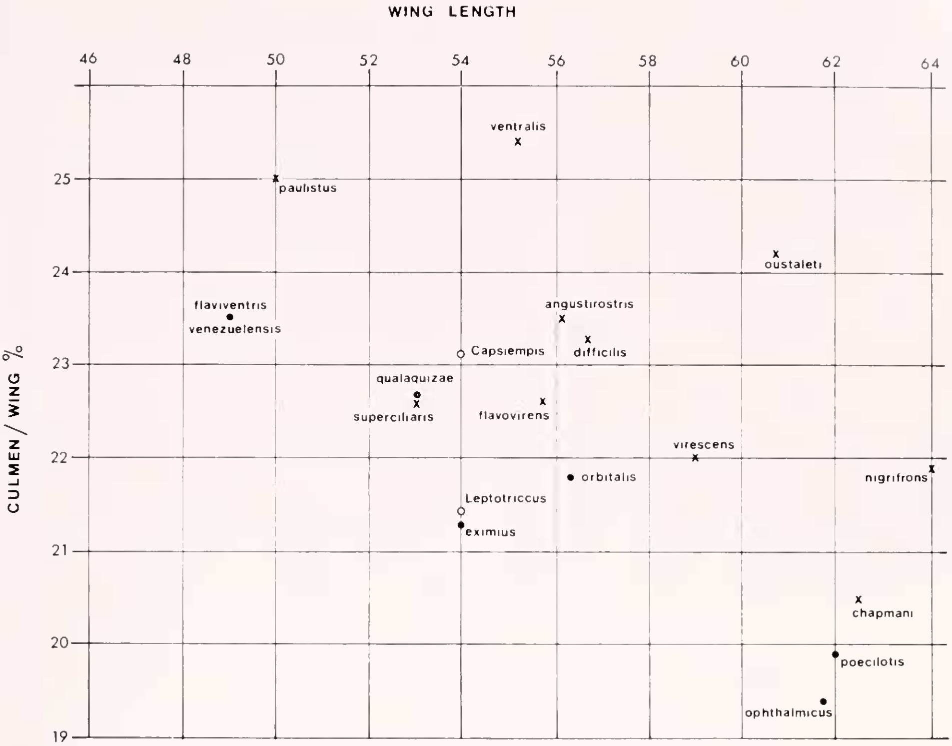

Figure 2. Proportions of culmen/wing plotted as functions of wing length. (See Fig. 1. legend.)

loscartes, but the former has a shorter tarsus, a type 3 nasal septum found otherwise only in the unrelated genera *Platyrinchus* and *Onychorhynchus*, and the peculiar nest type and single-wing flicking mentioned above. The importance of the nest type cannot be evaluated, since the nest type of only one of the 17 species in *Pogonotriccus* and *Phylloscartes* is known; *Phylloscartes ventralis* builds a partially domed, somewhat globular structure in the fork of a bough, according to Ihering (1904: 314).

Phylloscartes, *Pogonotriccus* and the two monotypic genera *Leptotriccus* and *Capsiempis* are a closely related group of genera placed by Berlepsch and Hellmayr in the Euscarthminae. They are all similar in appearance—small greenish and yellowish flycatchers, mostly with two well marked wing-bars, and several with gray crowns and patterned faces. All four were described as monotypic genera by Cabanis and Heine (1859: 52–56) for the type species *Phylloscartes ventralis*, *Pogonotriccus eximius*, *Leptotriccus sylviolus* and *Capsiempis flaveola*. The first three were defined primarily on mensural characters; *Phylloscartes* with a long bill and tarsus, *Pogonotriccus* with a long wing and short bill, and *Leptotriccus* by a "*Serpophaga*-like" bill and long tail. *Capsiempis* was considered more like *Tolmomyias flaviventer*, with a broad bill. During the next hundred years 15 species were added to this complex, seven by original description and eight by transfer from other genera, primarily *Leptopogon* and *Mecocerculus*. Within the group, two species, originally described in *Leptotriccus* and *Capsiempis* respectively, were moved to *Pogonotriccus*.

When the proportions of tail, culmen and

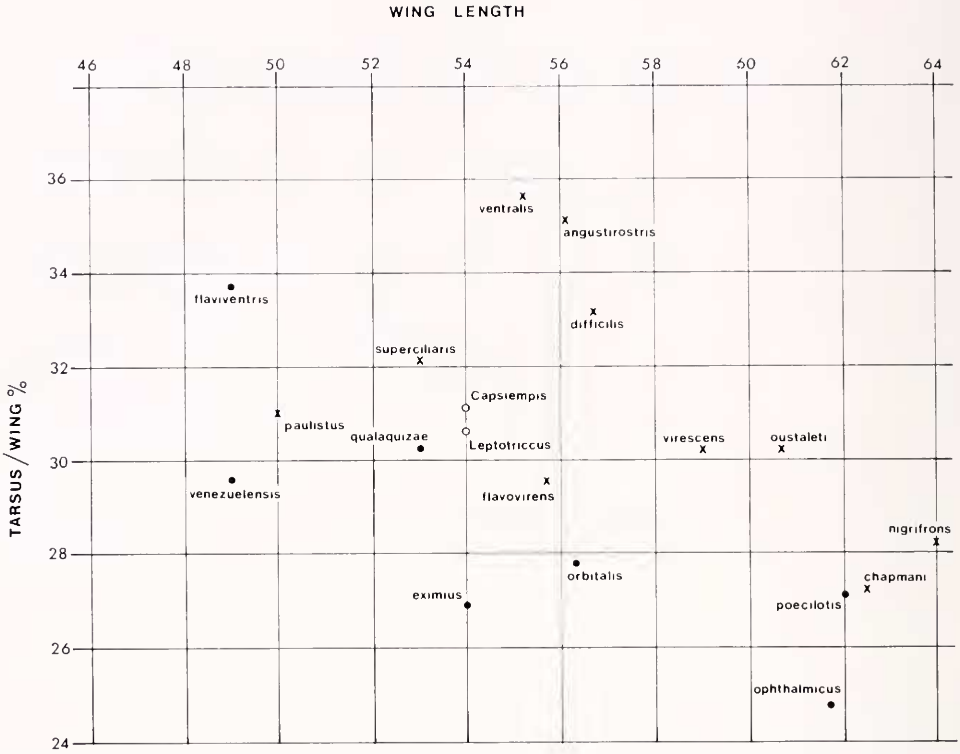

Figure 3. Proportions of tarsus/wing plotted as functions of wing length. (See Fig. 1. legend.)

tarsus to wing length are plotted as functions of wing length (Figs. 1–3), it is clear that on mensural characters the present genera overlap widely. There is a general trend within the group for species with longer wings to have proportionately shorter bills and tarsi, but this is true of all the currently recognized taxa. Even though some species are obviously separated from their nearest relatives by the present allocation to genera—the representative species *chapmani* and *poecilotis* being in *Phylloscartes* and *Pogonotriccus* respectively—no shifting of species between genera would segregate out two or more taxa. Warter (1965: 33) found the cranial characters similar in all four genera. Ames (1971: 67–72) considered the syrinxes different from each other and from all other genera, but as noted before negative syringeal evidence is inconclusive. I unite the four genera into a single genus. All the names were introduced at the same time in the same publication, and are equally available under the Rules [Art. 24(a)]. I select *Phylloscartes* as the name for the combined genus.

The geographical distributions of the species are most peculiar, but shed little light on relationships. Five species of *Pogonotriccus* are found in the subtropics of the Andes from Venezuela to Bolivia, but the sixth, the type *eximius*, is confined to the southeastern forest region of Brazil and adjoining Paraguay and Misiones, Argentina. On the other hand, four *Phylloscartes* species and *Leptotriccus sylviolus* are endemic to the southeastern forest region, and only the type, *ventralis*, has an isolated population in the Andean subtropics. The remaining species of *Phylloscartes* are found in the Guianan forests, the tepuis of

Venezuela, and in eastern Central America. Despite the fact that these are all forest forms, no species of this complex occurs in the Amazonian forests.

The one species that is out of place on ecological grounds is *Capsiempis flaveolus*, which has adapted to shrubs and bushes in clearings, and is found in the drier parts of tropical South America, north and west to Nicaragua. Eisenmann (*in litt.*) says that where *Capsiempis* overlaps the range of *Phylloscartes flavovirens* in Panama, the two are unlike in habits and do not appear closely related. However, as Zimmer (1940b: 2) pointed out, *flavovirens* and the closely related *virescens* are unusual among the *Phylloscartes* species in having more pointed wings, with the 10th primary equal to or greater than the 4th, rather than equal to or less than the 1st. *Pogonotriccus* species and *Leptotriccus* also have rounded wings with a short 10th primary. Practically nothing has been published about the habits of any *Phylloscartes* or *Pogonotriccus*, so it is not possible to say if *flavovirens* is typical of the rest of the genus. The only nests that have been described are *flaveolus* nests, which are cup-shaped, and *ventralis* nests which are partially covered. Although *Capsiempis* may later prove worthy of recognition as a distinct genus, I keep it in the enlarged *Phylloscartes* on morphological grounds.

Although the species of *Phylloscartes* do not have the long, spatulate-type bill characteristic of *Todirostrum* and *Idioptilon*, the bill is proportionately longer, and the rictal bristles more developed, than in the genera discussed so far. Their plumage pattern is typical of the "small green flycatchers" such as *Phyllomyias* and *Mecocerculus*, and they with *Leptopogon* represent the primitive stock from which the *Todirostrum* group evolved. Figure 4 is a schematic diagram showing the probable origin of the three best defined lineages within the Elaeniinae—the *Elaenia* group, the Tit-tyrants (*Anairetes*) and the Tody-tyrants. The position of *Pseudocolopteryx* and allies, and of *Pseudotriccus* is probably somewhere between the Tit-tyrants and the Tody-tyrants, although not part of the lineage of either; the position of the Flatbills, *Platyrinchus* and allies, is even less clear. *Phyllomyias*, *Mecocerculus*, and *Leptopogon* and *Phylloscartes*, the presumably primitive genera, resemble each other closely, although they lead into three distinct groups.

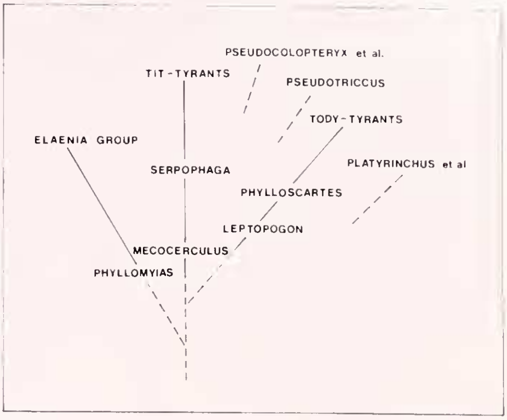

Figure 4. Schematic diagram showing probable relationships among the Elaeniinae. The three clearest lineages, *Elaenia* group, Tit-tyrants and Tody-tyrants, arose from *Phyllomyias*, *Mecocerculus*, and *Leptopogon* and *Phylloscartes*, respectively, genera that share a basic, "little green flycatcher" plumage pattern. The positions of genera not part of these lineages can only be suggested.

Pseudotriccus, including *Caenotriccus ruficeps* (Zimmer, 1940a: 22), is a peculiar genus of three species, confined to the subtropics of the Andes and extreme eastern Panama, that seems to have no close relatives among the genra of Hellmayr's Euscarthminae. It has generally been associated with *Hemitriccus* at the end of the *Todirostrum* group, but there is little real resemblance. The colors of *Pseudotriccus* are dull olive, olive brown or rufous, and the birds are without any embellishments such as streaking, superciliary stripes, eye rings, wing-bars or contrasting edgings to the flight feathers. All of the *Todirostrum* group and *Phylloscartes* have yellow under wing coverts that come around the edge of the wing, giving a bright spot at the bend when the wing is folded. In *Pseudotriccus* the under wing coverts are like the body plumage, with no contrast. The one genus to which *Pseudotriccus* may be allied is *Corythopis*, which has only recently been admitted to the Tyrannidae and which is without obvious relatives. The two genera share a proportionately long tarsus, relatively as long as those of the much smaller *Todirostrum/Idioptilon* species; the scutes of the tarsi are almost obsolete, giving a smooth booted effect; the wings are plain without any pale bars or edgings; and the rectrices are broad and soft. Fitzpatrick (in conversation) says they share similar feeding habits, walking along the ground and leaping up to pick insects from the under sides of leaves. I place *Corythopis* and *Pseudotriccus* together, and leave them between *Phylloscartes* and the *Todirostrum* group of genera, not because I am convinced that is where they belong, but because I know of no better place.

The genera I include in the term "*Todirostrum* group," as used above, are the remaining genera of Hellmayr's Euscarthminae: *Hemitriccus*, *Perissotriccus*, *Myiornis*, *Atalotriccus*, *Colopteryx*, *Lophotriccus*, *Idioptilon*, *Taeniotriccus*, *Poecilotriccus*, *Snethlagaea*, *Microcochlearius*, *Euscarthmornis*, *Oncostoma*, *Ceratotriccus* and *Todirostrum*. They are a closely related group, characterized by long slender tarsi, greater than 29 per cent of wing length, and long wide bills, greater than 25 per cent of wing length, culminating in the spatulate bill of *Todirostrum*. A generalized plumage pattern is found in at least some species of most genera: olive green or brown above; whitish below on throat and breast with darker streaking, and yellowish or olive on abdomen; remiges edged with olive or yellow. All species have yellow under wing coverts, which usually extend enough around the bend of the wing to make a yellow spot when the wing is folded. All recorded nests are of the pendent, purse-shaped or pyriform type.

Of the genera that Ames (1971: 67) examined all belonged in his *Colopteryx* group except *Todirostrum*. The cranial characters were alike in those genera that Warter (1965: 33) examined, but similar crania were found in *Phylloscartes* and *Pseudocolopteryx*, and in *Rhynchocyclus*, *Tolmomyias* and *Cnipodectes* of Hellmayr's Platyrinchinae. Zimmer (1940a: 13, 22) merged *Euscarthmornis* into *Idioptilon*, and *Perissotriccus* into *Myiornis*, and these changes were accepted by Meyer de Schauensee (1966).

Myiornis (including *Perissotriccus*) is a genus characterized by minute size; wing length in males averages less than 40 mm in all three species, and they are the smallest of the Tyrannids. Tail length is very short in *ecaudatus*, the type of *Perissotriccus*, but it is normal in *auricularis* and intermediate in *albiventris*. Bill and tarsal proportions fall into the normal range of the tody-tyrants.

Lophotriccus, *Colopteryx* and *Atalotriccus* have been placed together in the past, but the evidence for including *Atalotriccus* is equivocal. *Lophotriccus* is distinguished from the remainder of the tody-tyrants by its distinctive crest; the crown feathers are elongated and edged in contrasting gray or rusty. *Colopteryx galeatus* is the same as *Lophotriccus* in plumage, but has the three outer primaries much reduced. *Atalotriccus pilaris* has a normal crown, but has the four outer primaries even more reduced, narrowed and pointed. The plumage patterns and crest of *Lophotriccus* and *Colopteryx* are so much alike that the relationship must be close. I merge them here because I do not consider peculiar primaries a "generic" character in the flycatchers. *Atalotriccus* has been kept with *Colopteryx* because both have shortened outer primaries. If *Atalotriccus* has indeed been derived from *C. galeatus*, then the ornamental crest must have been lost secondarily. But it is just as easy to conceive *Atalotriccus* as an *Idioptilon* that has independently acquired reduced outer primaries and converged on *Colopteryx* in this character. The relatively long *Atalotriccus* tarsus is more like that of *Idioptilon* than that of *Lophotriccus*. Eisenmann (*in litt.*) believes *Atalotriccus* behaves more like *Todirostrum sylvia* than like *Lophotriccus*. Considering the doubts about the origin of *Atalotriccus*, I accept it as a distinct genus. Since this tody-tyrant group is uniform in cranial and syringeal characters, I doubt if further anatomical study will help clarify the relationships.

Fitzpatrick (1976) has just published a valuable paper on *Todirostrum* and related genera. He construed somewhat more strictly the concept of "related genera," and his study omits the following genera listed above: *Hemitriccus*, *Myiornis*, *Atalotriccus*, *Colopteryx* and *Lophotriccus*. Fitzpatrick attempted to trace the lineage and generic relationships of his tody-tyrants, and he made the following taxonomic suggestions:

1. The genus *Ceratotriccus* should be merged with *Idioptilon*.
2. The genera *Taeniotriccus* and *Poecilotriccus* should be moved to positions immediately preceding *Todirostrum*, reflecting their affinities with *Todirostrum capitale*.
3. *Todirostrum* and *Idioptilon* should continue to stand as separate genera.
4. The genera *Snethlagaea* and *Microcochlearius* are best merged with *Idioptilon*, while *Oncostoma* should continue to be generically recognized.

Fitzpatrick's lineage is shown diagrammatically in Figure 5, reprinted from his Figure 4 (p. 443). The genera that he does not consider, *Myiornis*, *Atalotriccus*, *Colopteryx* and *Lophotriccus*, would branch off further down the stem, on the way to the more highly specialized *Todirostrum*. With the exception that I consider *Hemitriccus* to belong to the "green" section of *Idioptilon*, I believe Fitzpatrick's tree accurately depicts the evolution and relationships of the tody-tyrants.

If his diagram is correct, then his taxonomic treatment of the *capitale* group, including *Todirostrum capitale*, *Taeniotriccus andrei* and *Poecilotriccus ruficeps*, must be questioned. These three species are united by a unique plumage pattern with chestnut crown, and by the striking sexual dimorphism in *capitale* and *andrei*. As Fitzpatrick says (p. 441), "Affinities among the three species are closer than those between the lineage as a whole and *Todirostrum* or *Idioptilon*." If this is so, the resemblance between the bill of *capitale* and those of *Todirostrum* species must be due to convergence, and placing *capitale* in *Todirostrum* makes that genus polyphyletic. Fitzpatrick recognized that the three species might possibly belong in a genus of their own, but hesitated to make such a major taxonomic shift without further anatomical and behavioral study. However, I believe the data require such a move now, and I place *capitale*, *andrei* and *ruficeps* in a separate genus for which *Poecilotriccus* is the oldest name.

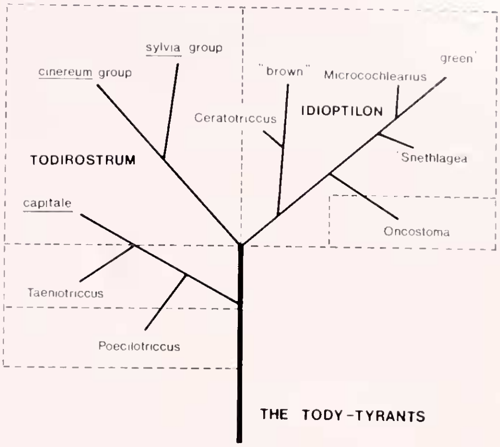

Figure 5. Fitzpatrick's (1976, Fig. 4) tree showing the lineage of the tody-tyrants. The stem to the lower left, leading to *Todirostrum capitale*, is here considered a single genus, *Poecilotriccus*.

Hemitriccus has been kept separate from *Idioptilon* because of the former's allegedly longer tail, and because of the slightly shortened 7th primary in males. While tail length in *H. diops* is proportionately longer than that of any *Idioptilon* species, the same is not true of *H. flammulatus* whose tail length is well within the normal *Idioptilon* range. In males the 7th primary is slightly shorter than the 6th and 8th, so the edge of the opened wing shows a slight notch rather than a smooth contour; the female wing is normal. Considering the variation in primaries within such genera as *Pseudocolopteryx*, this characteristic hardly rates generic separation. Plumage characters are like those of *Idioptilon*, and female *H. flammulatus* can hardly be told from the sympatric *I. zosterops griseipectus.* Merging *Hemitriccus* with *Idioptilon* will lead to yet another unfortunate change in the name of this beleaguered genus. Known as *Euscarthmus* to Sclater (1888) and Berlepsch (1907), it was *Euscarthmornis* to Hellmayr (1927), *Idioptilon* to Meyer de Schauensee (1966), and *Cerototriccus* to Fitzpatrick (1976); it must now be called *Hemitriccus*, the oldest available name.

To summarize the *Todirostrum* group, the sequence of the genera and their synonymies will be:

Myiornis (syn: *Perissotriccus*)
Lophotriccus (syn: *Colopteryx*)
Atalotriccus
Poecilotriccus (syn: *Taeniotriccus*)
Oncostoma
Hemitriccus (syn: *Idioptilon*, *Euscarthmornis*, *Snethlagaea*, *Microcochlearius*, *Ceratotriccus*)
Todirostrum.

Hellmayr's Platyrinchinae—*Platyrinchus*, *Rhynchocyclus*, *Tolmomyias*, *Ramphotrigon* and *Cnipodectes*—have occupied a position between the "large" flycatchers and the *Todirostrum* group since Berlepsch (1907), although *Platyrinchus* was put with the Todirostrines by Berlepsch, and with *Rhynchocyclus et al.* by Hellmayr. Warter considered that on cranial characters the Platyrinchinae graded into the Euscarthminae via *Todirostrum* and *Oncostoma*, but in general form and appearance, they do not seem closely related to any other genus or group of genera. They have been kept together in part because of their broad, flat bills, moderate to heavy rictal bristles and fairly short, slender tarsi, but in the case of *Platyrinchus*, these are probably convergent characters. The bills of *Rhynchocyclus* and *Tolmomyias* are the extremes of broad and flat but swollen-appearing bills with strongly convex lateral edges; *Cnipodectes* is somewhat narrower at the base, and *Ramphotrigon* even more so, with the lateral edges straight. *Platyrinchus* has the same broad, convex bill, but it is much flattened.

Rhynchocyclus and *Tolmomyias* resemble each other closely externally, the latter seeming a smaller version of the former. However, Ames (1971: 161) found they "differ so strongly in their syringeal structure that one may seriously question the reliability of bill shape as a common character." Also, Skutch (1960: 515) has pointed out well-marked differences in mating behavior, egg coloration and the extent of down on the nestlings. *Cnipodectes* is close to these two, but its brown coloration, uniquely twisted primaries in the male, and extreme sexual dimorphism merit recognition. In plumage pattern, *Ramphotrigon* species, particularly *fuscicauda*, look very much like *Rynchocyclus*, but the bill is slender and straight edged, the mandible is blackish rather than pale horn (in dried skins), and they have two well-marked buffy or chestnut wing-bars, which are not found in *Rhynchocyclus*. Ames (1971 : 161) supported Zimmer's (1939c: 16) transfer of *megacephala* from *Tolmomyias* to *Ramphotrigon.* He found the syrinx of *megacephala* strikingly different from that of *Tolmomyias sulphurescens.* The *Ramphotrigon* nest has not been described; *Rhynchocyclus* and *Tolmomyias* make pendent retort-shaped nests (Smithe, 1966: 322), and *Cnipodectes* makes a pendent nest whose completed shape is not known (Wetmore, 1972: 508).

As noted before, *Platyrinchus* does not fit easily into this assemblage. The species all have short tails, less than 50 per cent of wing length, a pale patch on the throat, pale instead of blackish feet and tarsi and brightly colored crests; they all build cup-shaped rather than pendent nests. *Platyrinchus* has a type 3 nasal septum, found elsewhere only in *Onychorhynchus* and *Leptopogon*, while *Cnipodectes, Tolmomyias* and *Rhynchocyclus* have type 1. However, in the last three, the nasal septum evidently approaches the type 3, so the difference may not be so great as it appears at first glance. The syrinx of *Platyrinchus* most resembles that of Ames' *Colopteryx*, and is not at all like that of *Tolmomyias* or *Rhynchocyclus.* Although the relations of *Platyrinchus* are almost certainly with the Elaeniinae, it does not seem closely related to any of the other genera, and I leave it at the end of the subfamily.

FLUVICOLINAE

The subfamily Fluvicolinae as now constituted, with the addition of the major part of the old Myiarchinae, has a number of genera that in size and plumage pattern resemble the more generalized Elaeniinae. Such genera as *Myiobius* and *Myiophobus* are close in size, proportions and plumage pattern to the Elaeniine *Phyllomyias* and *Phylloscartes.* Externally they are best distinguished by the broad, triangular flattened bill and heavy rictal bristles; internally they all have Warter's type 6 nasal septum, which occurs elsewhere only in *Polystictus* and *Zimmerius*, where it has almost certainly been derived independently. Within the Fluvicolinae there appear to be two lineages. The first starts with *Myiobius, Myiophobus* and allies, and leads to *Empidonax, Contopus* and *Sayornis*, which have speciated extensively in North and Central America. The second starts with the generalized *Ochthoeca* and runs through the highly successful *Xolmis* and *Muscisaxicola* to a number of truly aberrant genera such as *Muscigralla*; the center of speciation and generation in this lineage has been southern South America. Besides being separable on external morphological and zoogeographical grounds, the members of the North American lineage, except for *Myiophobus, Cnemotriccus* and *Nuttallornis*, all have type 3 palatines, while none of the South American lineage have them.

I begin the Fluvicolinae with *Onychorynchus*, a genus that is highly specialized but apparently is an early offshoot of the primitive stock. Both sexes of *Onychorhynchus* have long, elaborate transverse crests, red or yellow tipped with iridescent blue or violet, and long, broad, flattened bills with heavy rictal bristles reaching the tip of the bill. Ames (1971: 160) placed *Onychorhynchus* in the *Myiobius* group with *Terenotriccus* and *Pyrrhomyias*, but Warter (1965: 37) made it a monotypic tribe in his Platyrinchinae, and said it most resembled *Platyrinchus* and *Tolmomyias. Onychorhynchus* shares the type 3 nasal septum with *Platyrinchus*, and this type is also suggested in *Tolmomyias.* However, *Onychorhynchus* lacks the type 4 interorbital septum, which characterizes the Elaeniinae in general and is found in *Platyrinchus* and allies. On external morphology, Hellmayr placed *Onychorhynchus* near *Myiobius*, and they certainly share the most extreme development of the rictal bristles, which extend beyond the tips of the broad flat bills. The syringeal evidence supports this association of the two genera. I keep *Onychorhynchus* in the Fluvicolinae, even though it is the only genus in the subfamily, except for the aberrant *Muscigralla*, that does not have a type 6 nasal septum.

Wetmore (1972: 532) notes that the eggs of *Onychorhynchus* and *Lophotriccus* resemble each other in having a "bright to dark reddish gray ground color, thickly marked with carmine in scrawling lines," a type not found elsewhere among the Tyrannidae. This suggested to him that a possible relationship might exist between the genera. Eisenmann (*in litt.*) notes that *Lophotriccus* displays its crest in hostile situations in the same manner as *Onychorhynchus*, by spreading it laterally, opening its beak, and rotating the head through 180°. Although these shared characters are suggestive, they are not supported by any anatomical or external morphological characters. The two genera do not share any of Warter's cranial characters, and Ames has them in different syringeal groups—*Onychorhynchus* in his *Myiobius* group without intrinsic muscles, and *Lophotriccus* in his *Colopteryx* group with intrinsic muscles. Externally, *Onychorhynchus* is much larger, with wing length about 60 per cent longer than that of *Lophotriccus*, and has a proportionately longer bill, about 32 per cent of wing length compared to about 25 per cent in *Lophotriccus*. The tarsus of *Onychorhynchus* is comparatively much shorter than that of *Lophotriccus*, and the most striking difference in proportions is seen in the ratio culmen tarsus, which is about 155 per cent in *Onychorhynchus* and about 80 per cent in *Lophotriccus*. Although the long crests are used in the same way, they seem to have evolved differently. That of *Onychorhynchus* appears to have developed from a bright orange or yellow crown of the type found in *Tyrannus*, being composed of bright feathers greatly lengthened and tipped with iridescent blue. The crest of *Lophotriccus*, on the other hand, is made up of lengthened ordinary crown feathers, edged with rusty or gray. Both genera make pensile nests, but this is true of all their potential relatives, *Myiobius*, *Rhynchocyclus* and Ames' *Colopteryx* group. Although it is unusual to find simultaneous convergence in two such unrelated characters as egg color and crest display, I do not believe that *Onychorhynchus* is closely related to *Lophotriccus*.

The genera *Myiobius* and *Terenotriccus* form a natural group because they and *Onychorhynchus* are the only genera of Fluvicolines to make a pendent, purse-shaped nest, similar to that found in the *Todirostrum* group of the Elaeniinae. *Myiotriccus* closely resembles *Myiobius* in form and plumage pattern, and I include it here even though its nest is unrecorded. I do not merge the two because *Myiotriccus* is more brightly colored and lacks the heavy rictal bristles, extending beyond the bill tip, that are characteristic of *Myiobius*. This group of genera is related to *Onychorhynchus* on the one hand and to *Pyrrhomyias* on the other by their peculiar syringes, in which there are no intrinsic muscles.

The remaining genera of Warter's "Contopini," formerly in the Myiarchinae of Hellmayr, are an unusually difficult group to order lineally. The majority seem to have characters relating them to two or more of the others, and there are a few about which little is known that must be inserted next to their apparent nearest relatives, thereby interrupting an otherwise orderly progression. Webster (1968), in his review of the genus *Mitrephanes*, suggested the following sequence for the genera that he considered closely related (I invert his sequence to make it comparable with mine): *Empidonax, Xenotriccus, Pyrrhomyias, Mitrephanes, Contopus, Nuttallornis*. I agree with this sequence, except that I would place *Empidonax* at the other end, next to *Contopus* and *Nuttallornis*. Not only are these genera close in appearance, but an intergeneric hybrid between *Contopus* and *Empidonax* has been recorded by Short and Burleigh (1965). My sequence, including those genera not considered by Webster, is *Myiophobus, Aphanotriccus* (including *Praedo*), *Xenotriccus* (including *Aechmolophus*), *Pyrrhomyias, Mitrephanes, Contopus* (including *Nuttallornis* and *Blacicus*), *Empidonax, Nesotriccus, Cnemotriccus, Sayornis* and *Pyrocephalus*.

Myiophobus is a genus that is superficially like *Myiobius*, but probably not closely related. The two are similar in proportions and general appearance, but *Myiophobus* lacks the bright crest and rump characteristic of *Myiobius*, and makes a cup-shaped rather than a pensile nest. *Myiophobus* is not placed by Ames in any of his syringeal groups, but *Myiobius* is part of the group lacking intrinsic muscles. It is risky to generalize about *Myiophobus*, because the only species for which the syrinx and cranium were available, and whose nest and habits have been recorded, is *fasciatus*, the least typical ecologically. Of the nine species of *Myiophobus*, all but *fasciatus* are found in the subtropical zone of the Andes, where several have notably restricted and fragmented ranges. On the other hand, *fasciatus*, is found throughout the drier lowlands of South America, even reaching Costa Rica.

Aphanotriccus (including *Praedo*) and *Xenotriccus* (including *Aechmolophus*) are each composed of two relict species with restricted ranges in Central America and adjoining Colombia. Both were included in Ames' *Nuttallornis* group of genera on syringeal characters. The species of *Aphanotriccus* show the same type of color variation, in which cinnamon and olive replace each other, as is found in *Pyrrhomyias* and *Mitrephanes*. One species of *Xenotriccus* is dull colored like *Contopus*. Their relict distribution suggests they may be remnants of an earlier stock from which the currently successful Central and North American genera *Contopus*, *Empidonax* and *Sayornis* were derived.

Pyrrhomyias cinnamomea is a difficult genus and species to place because it combines the peculiar syrinx of Ames' *Myiobius* group, which lacks intrinsic muscles, with the form and coloration of *Mitrephanes*. In the *Myiobius* group it would be the only species that makes a cup-shaped instead of a pendent nest and has a pointed instead of a much rounded wing, with 10th primary equal to the 5th or 6th in length, rather than shorter than the first. In its pointed wing, and even more, in its comparatively very short tarsus, it agrees with *Mitrephanes* and *Contopus*. I can find nothing recorded on the habits of *cinnamomea*, an Andean subtropical species from Venezuela to Bolivia, but *Mitrephanes phaeocercus* is reported by Webster (1968) and Eisenmann (*in litt.*) to be a miniature *Contopus* in habits.

Contopus (including *Nuttallornis* and *Blacicus*), *Empidonax*, *Pyrocephalus* and *Sayornis* comprise what I have been calling the Central and North American genera. All but *Pyrocephalus* were included in Ames' *Nuttallornis* group on the basis of syringeal characters. Warter (1965: 36) also removed *Sayornis* and *Pyrocephalus* from Hellmayr's Fluvicolinae to the vicinity of *Contopus* and *Empidonax* on cranial characters. The removal of *Sayornis* from the restricted Fluvicolinae on zoogeographical grounds was suggested by Ihering in 1904 (p. 320), but his idea was ignored by Berlepsch and Hellmayr. Actually, placing *Sayornis* near *Contopus* and *Empidonax* is a familiar arrangement to North American ornithologists, because the American Ornithologists' Union Checklist (1957) and Mayr and Short (1970) place it there.

Sayornis and *Empidonax* are the most truly North American flycatchers. All three species of *Sayornis* breed in North America, and one of them, *nigricans*, has recently invaded South America along the Andes, where it differs only subspecifically. There are 10 species of *Empidonax* breeding in North America, six in Central America and only two in South America; possibly the latter represent an invasion from the north, but the evidence is not so clear as in the case of *Sayornis nigricans*. The species of *Contopus* are more evenly distributed geographically, but the genus is closely related to *Empidonax*, as witness an intergeneric hybrid reported by Short and Burleigh (1965). Considering present distribution, *Contopus* may well have been the primitive stock from which the others were derived. *Pyrocephalus* has a wide but disjunct range from southern North America through drier tropical South America, and even in the Galapagos; its geographical origins are not clear, but it bears a close resemblance in general form and in cranial characters to *Sayornis*.

Cnemotriccus fuscatus is found throughout the tropical lowlands of South America. In plumage, *fuscatus* is very close to *Empidonax*, but it has a white superciliary instead of the white eye-ring characteristic of that genus, and has also a blackish mandible and a rounded rather than square tail. Hellmayr (1927: 225) included *poecilurus* in *Cnemotriccus* but Zimmer has shown (1937b: 26) that this species is a hen-colored *Knipolegus.* Proportions are so constant within the medium-sized Fluvicolinae that plumage pattern and color and bill form are frequently the best guides to relationships.

Nesotriccus ridgwayi, the endemic genus and species of Cocos Island, seems to fit best in the vicinity of *Cnemotriccus* and *Empidonax*, despite cranial evidence to the contrary. *Nesotriccus* has always been assumed to be an island representative of *Myiarchus*, but the reasons are more inferential than logical. The Geospizinae of the Galapagos have an obvious representative in *Pinaroloxia* of Cocos Island, and when an endemic flycatcher was discovered on Cocos, it was assumed (Townsend, 1895: 124) to be a representative of *Eribates* (= *Myiarchus*) *magnirostris* of the Galapagos. *Magnirostris* is a typical *Myiarchus* in plumage, and differs only in having the proportionately longer bill and tarsi characteristic of island forms. *Nesotriccus*, however, is not at all Myiarchine in plumage, but most nearly resembles *Empidonax euleri* or *Cnemotriccus fuscatus* in both adult and juvenal plumages. The bill and tarsi are even more lengthened proportionately than in *Eribates.* The nest form would give the best evidence of affinities, but unfortunately the nest of *Nesotriccus* is unknown. Swarth (1931: 84), comparing the behavior of *ridgwayi* and *magnirostris* writes, "The supposed resemblance between these two species is non-existent to me," and Slud (1967: 286) says *Nesotriccus* suggested to him a long-billed, slim *Empidonax*; it moved about in the foliage in finch-like hops and spurts, and proved itself adept at aerial feeding, making flickering short sallies. *Nesotriccus* lacks the type 6 nasal septum characteristic of the Fluvicolinae, but its other cranial characters are sufficiently mixed that Warter (1965: 37) considered it intermediate between *Myiarchus* and *Todirostrum.* I shall leave *Nesotriccus* between *Cnemotriccus* and *Empidonax.*

The mergings of genera indicated above have all been previously suggested. *Nuttallornis* has been merged with *Contopus* by Phillips, Marshall and Monson (1964: 90) and *Blacicus* was placed in *Contopus* by Bond (1943: 117). *Aechmolophus* was made a synonym of *Xenotriccus* by Webster (1968: 289). *Praedo* was made a synonym of *Aphanotriccus* by Griscom (1929: 176) although Wetmore (1952: 487) continues to recognize the former.

The remainder of the Fluvicolinae are the South American element that historically made up the restricted subfamily of that name. It is composed of a number of specialized, terrestrial genera with numerous sympatric species, some more generalized, arboreal forms and several distinctive monotypic genera. Despite the great variation in size, proportions, plumage and behavior, the Fluvicolines seem a closely related group. Ames (1971: 158) includes a broad spectrum of genera in his *Fluvicola* group, which is of more significance than the fact that many closely related genera were not part of the group. Warter found that, with the exception of *Muscigralla*, all had a type 6 nasal septum, and types 1 or 2 palatines. Geographically, all belong to the dry country or temperate zones of South America, or are specialized for marshes or riverine habitats. None occur in the humid forests of Amazonia, although *Muscisaxicola fluviatilis* and *Ochthoeca* (*Ochthornis*) *littoralis* are found on beaches and on edges of Amazonian waterways.

Smith and Vuilleumier (1971) reviewed the evolutionary relationships of a number of the ground tyrants; Vuilleumier used evidence from external morphology and ecology and Smith from behavior. They included in their study the following genera of Hellmayr: *Agriornis, Xolmis, Muscisaxicola, Myiotheretes, Cnemarchus,* *Neoxolmis, Ochthodiaeta, Ochthoeca* and *Muscigralla.* In their conclusions they merged *Myiothretes, Cnemarchus* and *Octhodiaeta* with *Xolmis*; they also kept *Pyrope* in *Xolmis* as Hellmayr had it, although Zimmer (*Ms.*) and Meyer de Schauensee (1966: 335) recognized it as a distinct genus. *Muscigralla* was made a subgenus of *Muscisaxicola*, and the species *murina* was transferred from *Xolmis* to *Agriornis.* Their sequence of genera was *Ochthoeca, Xolmis, Neoxolmis, Agriornis* and *Muscisaxicola*, since they considered the arboreal or bush haunting genera more primitive or generalized than the puna or steppe inhabiting terrestrial forms.

I agree with Smith and Vuilleumier's exposition of the relationships among these "ground tyrants," but I feel they have gone too far in lumping some of the genera. All the species included in Hellmayr's *Myiotheretes, Cnemarchus* and *Ochthodiaeta* are characterized by brown, buff or rusty plumage, and are found only in brush or the edge of forest in the high Andes, from Venezuela to northwestern Argentina. The species of Hellmayr's *Xolmis*, on the other hand, are with one exception patterned in black, gray or white and are found in tropical to temperate lowlands from eastern Brazil and Bolivia south to Patagonia. I feel that the dichotomy between these two groups is so marked that, even though they may have had a common ancestor, their present relationship is best shown by the recognition of two genera—*Myiotheretes* (including *Cnemarchus* and *Ochthodiaeta*) and *Xolmis.*

The one exception to the black, gray and white plumage pattern in *Xolmis* is *rubetra*, which is brown above with a russet crown, and whitish below, streaked dark brown on throat and breast, and with a russet wash on the flanks. Vuilleumier (in Smith and Vuilleumier 1971: 197) says, "In color, pattern and habits, *X. rubetra* is intermediate between the other species of *Xolmis* and *Neoxolmis rufiventer*, and may represent an evolutionary transitional "stage" between arboreal and terrestrial tyrants." *Neoxolmis* is almost wholly terrestrial in habits, only occasionally perching on low bushes, and it was for this reason, along with the proportionately longer tarsus associated with terrestrial habits, that Vuilleumier recognized it. *Rubetra* is the most terrestrial of the *Xolmis* species, with a tarsus proportionately as long as in *rufiventris*, and its plumage is not far from the female plumage of *rufiventris*. *Rubetra* and *rufiventris* have allopatric breeding ranges, the former in northern Patagonia from Mendoza to Chubut, the latter in southern Patagonia and Tierra del Fuego. I believe that transferring *rubetra* from *Xolmis* to *Neoxolmis* best shows the relationships of these forms.

In the remainder of the genera treated, I accept Smith and Vuilleumier's revision with a single exception, the inclusion of *Muscigralla* in *Muscisaxicola.* As discussed in more detail below, I find the former so distinct morphologically that I cannot consider it closely related to any other genus. I have also accepted Vuilleumier's (p. 192) tentative suggestions that the monotypic genera *Ochthornis* and *Colorhamphus* be merged in *Ochthoeca. Ochthornis littoralis* is a riverine species found throughout Amazonia, while the species of *Ochthoeca* are found in temperate Andean forest or scrub. *Littoralis* is dull brown throughout, but with the white superciliaries of *Ochthoeca*; in proportions it has a longer bill and shorter tarsus than the Andean forms. In plumage and proportions it bears the same relation to *Ochthoeca* that *Muscisaxicola fluviatilis* (also a riverine form of Amazonia) bears to the remaining Andean species of its genus, and I place *Ochthornis* in *Ochthoeca. Colorhamphus parvirostris* has been kept in the Serpophaginae (now Elaeniinae), but it also appears to be a dulled *Ochthoeca.* Cranial characters, which might give more positive evidence, are lacking. In size and proportions *parvirostris* is identical with *Ochthoeca rufipectoralis*; however, in plumage it is closest to *oenanthoides*, of which it appears to be a geographical representative. *Oenanthoides* breeds south through the Andes to the mountains of northwestern Argentina, while *parvirostris* replaces it in Patagonia and Fuegia. Vuilleumier (*loc. cit.*) also suggested that *Tumbezia* be included in *Ochthoeca*. The former has a more slender bill and more pointed wing than the *Ochthoecas*, and inhabits the arid coastal zone of Peru along with the peculiar *Muscigralla*. Although these are not trenchant characters, *Tumbezia* does not suggest *Ochthoeca* to me, and I keep it monotypic.

Lessonia appears to be a link, phenotypically at least, between the terrestrial *Muscisaxicola* and the more arboreal *Knipolegus*. In form the *Lessonia* species are similar to *Muscisaxicola*, with long tarsi and pointed wings; they are completely terrestrial, and have a lengthened hind claw like many of the pipits (*Anthus*). On the other hand, they are markedly sexually dimorphic, the males are mostly black and the females brownish like the majority of *Knipolegus*.

In *Knipolegus* I include *Phaeotriccus* and *Entotriccus*, two genera showing the same type of sexual dimorphism, blue-black bill and form as *Knipolegus*, but separated from the latter by the narrow, blade-shaped outer primaries. In *Phaeotriccus* the three outer primaries are narrowed, as are all in *Entotriccus*, but aberrant primaries vary intragenerically so often in the flycatchers, that by themselves they serve only as specific characters. Short (1975: 269) has also suggested merging the three.

Hymenops (*Lichenops* in Hellmayr) is intermediate between *Knipolegus* and the palustrine *Fluvicola* and *Arundinicola*. In plumage it is similar to *Knipolegus*, having a black male and a brown female with heavily streaked white underparts. However, the male has a bright yellow bill and yellow caruncles around the eye, and both sexes have a short, rounded wing, with the 7th secondary almost reaching the wing tip. *Hymenops* is palustrine, as are *Fluvicola* and *Arundinicola*. The latter two, although differing in proportions and wing form, are so alike in their black and white or brown and white plumage, palustrine habitat and nest form, that I feel they must be united under the oldest name, *Fluvicola*.

Following *Fluvicola* is a group of four fancy-tailed tyrants that Warter (1965: 130) thinks should be treated as a distinct tribe, Alectrurini, within the Fluvicolines. At present they are kept in four monotypic genera, *Colonia*, *Gubernetes*, *Alectrurus* and *Yetapa*. *Colonia*, with its black and white plumage, seems to link this group with *Fluvicola*, although Ames said the syrinx of *Colonia* was unlike *Fluvicola* and more nearly like *Ochthoeca*. *Colonia* differs from the other three species in having the central instead of the outer rectrices developed into ornamental plumes, and in being a short-billed, short-legged, arboreal, hole-nester, rather than a long-billed, long-legged, terrestrial, ground-nester. *Gubernetes*, *Alectrurus* and *Yetapa* have always been considered closely related. The last two should be merged as suggested by Short (1975: 269); the only differences are in the shape of the ornamental rectrices, and the fact that the male of *A. tricolor* loses the feathers of the face during the breeding season. *Gubernetes* is much larger, lacks the black and white plumage found in the males of *Alectrurus*, and has a forked tail like *Muscivora tyrannus* rather than ornamental outer rectrices. I keep it as a distinct genus. While I accept the near relationship of *Colonia*, *Gubernetes* and *Alectrurus* as shown by the cranial characters, I do not consider them more distinct than the other groups of Fluvicoline genera.

There remain in the Fluvicolinae six monotypic genera that are kept together not because they are necessarily related to each other, but because none of them seems to have any demonstrable close relative. They are: *Satrapa*, *Tumbezia*, *Muscigralla*, *Hirundinea*, *Machetornis* and *Muscipipra*. The first two may be related. Both have dark, uniform upperparts, olive green in

Satrapa and brown in *Tumbezia*, and both have a yellow forehead, superciliaries and underparts. *Satrapa*, however, is a larger bird with proportionately much shorter tarsus—20.5 per cent of wing length compared to 29 per cent. *Tumbezia* occurs on the arid Peruvian coast and *Satrapa* in the dry country east of the Andes and south of Amazonia. They may, as noted before, turn out to be related to *Ochthoeca*.

Smith and Vuilleumier (1971) made *Muscigralla* a subgenus of *Muscisaxicola*. However, *Muscigralla brevicauda* is unlike any *Muscisaxicola* in proportions and plumage pattern, and has tarsal scutellation unlike any flycatcher. It has rounded wings rather than the very pointed wings of *Muscisaxicola*, a proportionately short tail, and much longer culmen and tarsus. Unlike the species of *Muscisaxicola*, which have uniform dull brownish backs and blackish tails and tail coverts, *brevicauda* has pale buff tipping on the rump feathers, bright chestnut uppertail coverts, and a blackish tail tipped with pale buff. It also has a concealed yellow crest of a type not found in *Muscisaxicola*. The most distinctive differences, however, are found in the tarsi. All *Muscisaxicola* have typically exaspidean tarsi, with at most a few scutes on the proximal half of the plantar surface; there is a deep groove on the inner surface where the scutes meet, but none on the outer surface, and the scutes are smooth. *Muscigralla* has a classic holaspidean tarsus, with a deep groove on both inner and outer surfaces, and the distal edges of the scutes are raised, giving a roughened serrate feel. Furthermore, this scutellation extends for about 10 mm above the tibio-tarsal joint as in the shorebirds, a condition found in no other flycatcher. Ames (1971: 160) believed its syrinx was most nearly related to *Nuttallornis* and not the Fluvicolinae. Warter (1965: 36) found it to be a good Tyrannid, but (p. 31) listed it as the only Fluvicoline without a type 6 nasal septum. Its geographic range, the arid coast from Ecuador to southern Peru, is typical of species in several groups. Despite the fact that Smith and Vuilleumier (1971: 201, 253) and Fitzpatrick (*in litt.*) consider its displays and vocalizations closely related to those of *Muscisaxicola*, I cannot see that *Muscigralla* has any close relatives; morphologically and anatomically it is not typical of the Fluvicolines. On the other hand, it is equally out of place in any other group, and considering its generally brownish color, terrestrial habits and restricted non-forest range, it was probably an early offshoot of the Fluvicoline stock, and I shall keep it at the end of that group with other aberrant genera.

Hirundinea is a monotypic genus placed by Berlepsch (1907) without comment between *Myiobius* and *Onychrorhynchus* at the end of the Myiarchinae. I cannot see any relationship with that group. *Hirundinea ferruginea* is a pointed winged, aerial feeder with proportionately the shortest tarsus of any flycatcher, 12 per cent of wing length; the bill is long but the rictus only moderately bristled. It occurs in woodland and campos north and south of Amazonia, extending to northern Argentina and temperate Bolivia. It nests primarily on cliff faces, but in some areas it is virtually a commensal of man, placing its nest in niches of buildings or old oven bird nests, and it will sometimes wall off its nest with pebbles (Euler, 1900: 48). *Onychrorhynchus* and *Myiobius*, on the other hand, are round winged, forest haunting birds, with the heaviest rictal bristles of any of the flycatchers, and make long, pendent purse-shaped nests. In proportions, *Hirundinea* is more like the Tyrannine flycatchers with its pointed wing and short tarsi, but it is unlike any of that group in plumage and nesting habits. In distribution it is typical of the Fluvicolines, and I place it with the other peculiar monotypic genera of that group. Unfortunately, no one has had anatomical material available for study.

Machetornis rixosus is a rounded winged, long-legged, terrestrial species that in plumage pattern and in temperment is remarkably like the tropical kingbirds of the genus *Tyrannus.* It would be tempting to consider it a member of the latter group, secondarily adapted for terrestrial life, were it not for the fact that its cranium is typically Fluvicoline, and it does not share a single cranial character with the Tyrannines. Ames (1971: 147) says that the Mm. sternotracheales of *Machetornis* strongly resemble those of *Xolmis,* but that it lacks intrinsic muscles. He considered that if the relationship to the other "ground tyrants" was real, *Machetornis* must have lost its intrinsic muscles. The last of the aberrant Fluvicolines, *Muscipipra vetula,* is again much like the Tyrannine kingbirds, both in plumage and proportions. In absolute size and proportions it is very close to *Tyrannus savana* (*Muscivora tyrannus*), but it is dull gray rather than black and white, lacks any bright crest, and the fork of the tail is less deep. On the other hand, it shares the same proportions with *Colonia* among the Fluvicolines, and on the basis of syringeal characters, Ames (1971: 158) placed it in his *Fluvicola* group. Warter had no specimen and I can find nothing on its habits. Its restricted range in southeastern Brazil and adjoining Paraguay and Misiones, Argentina, tells us little. *Muscipipra* may well prove to be a Tyrannine, but in the absence of more concrete evidence, I leave it in the Fluvicolines.

TYRANNINAE

The remaining subfamily, Tyranninae, consists of Hellmayr's old Tyranninae plus *Myiarchus* and allied genera. While it is difficult to define the subfamily as advanced or specialized, it is certainly successful and is the one that appears to have undergone the most recent radiation. Almost all the genera and many of the species are found throughout Central and South America, and the majority are aggressive and dominant wherever found. The extreme uniformity of the crania is evidence of recent radiation; only two types of nasal septa occur, both without basal plates, and interorbital septa, palatines and cranial types are identical throughout.

Warter recognized Attilinae as a subfamily (1965: 95, 140) because of its peculiar cranial characters; it included *Attila,* and presumably *Pseudattila* and *Casiornis,* which Warter was unable to examine. However, as noted before, external morphology and syringeal characters strongly suggest that *Attila* (including *Pseudattila*), *Casiornis, Laniocera* and *Rhytipterna* are a closely related group of genera belonging with *Myiarchus. Rhytipterna* and *Myiarchus* in turn are clearly part of the subfamily Tyranninae, as evidenced by cranial characters. Despite the contrary cranial evidence separating *Attila* from the rest of the *Myiarchus* group, I believe the weight of evidence is in favor of keeping them all together.

I begin the Tyranninae with the *Myiarchus* group. *Syristes,* which has previously been placed near *Tyrannus* by Hellmayr (1927: 119), but in the Cotingidae by Ridgway (1907: 815), also belongs here. It has a holaspidean tarsus similar to *Casiornis* or *Rhytipterna,* and the cranial characters of *Syristes* and *Rhytipterna* are identical. Although the plumage is more like that of *Tyrannus,* the rounded wing, holaspidean tarsus and type 2 nasal septum place it with *Rhytipterna* and near *Myiarchus.* This is essentially the sequence of Wetmore (1972: 433), who put it between *Myiarchus* and *Attila. Hylonax* and *Eribates* are included in *Myiarchus. Deltarhynchus flammulatus,* which is pure *Myiarchus* in plumage, is separated from the latter by its short, triangular bill. Unfortunately nothing has been published on the anatomy or behavior of *flammulatus.* If it is found to be a hole nester, using a few scraps of snake skin for decoration, it should certainly be merged in *Myiarchus.*

The remainder of the genera are those included by Hellmayr in his Tyranninae. Although they are related to the *Myiarchus* group through identical interorbital septa, palatines and crania, they differ, with the exception of *Legatus*, in having a type 1 instead of a type 2 nasal septum, and the majority belong to the *Tyrannus* syringeal group rather than the *Myiarchus* group.

Meise (1949) reviewed Hellmayr's Tyranninae, and separated the genera into three groups on the basis of nest type. They were: 1) those with open, bowl-shaped nests—*Tyrannus* (including *Tyrannopsis* and *Tolmarchus*), *Muscivora*, *Empidonomus*, *Legatus*, *Conopias* (including *Coryphotriccus*) and *Megarhynchus*; 2) hole nesters—*Myiodynastes*; and 3) those with globular nests—*Myiozetetes* and *Pitangus*. Although Meise's classification is a useful approach, increasing knowledge has made some of his conclusions questionable. *Conopias parva* turns out to nest in holes and nested at least once in an abandoned cacique nest (Haverschmidt 1957: 240; 1973: 207). Within the genus *Pitangus*, *sulphuratus* makes a globular nest and *lictor* usually a cup-shaped nest. The nest described for *Conopias inornata* by Cherrie (1916: 238), a small cup, saddled on a branch and neatly covered with lichens, is totally unlike the loose, stick nests in forks or crotches characteristic of other cup-nest builders in this subfamily. Finally *Legatus* usurps the domed nests of many species from different families, annoying the owners until they abandon the completed nest (Skutch, 1960: 451; Haverschmidt 1968: 305). Although nest type is an important character, it cannot be the primary basis for a classification.

There are five currently recognized genera in which the same distinctive plumage pattern occurs in at least one species. These are *Pitangus*, *Myiozetetes*, *Conopias*, *Myiodynastes* and *Megarhynchus*. The plumage characteristic of this group of genera has the crown blackish with a concealed yellow or orange crest; white forehead and superciliaries, with the latter usually extending around to meet on the nape; broad black band through the eye; upperparts olive to brown, in contrast with the dark crown; wings and tail brown, the feathers edged with the color of the back or with chestnut; throat white or yellow; breast, belly and crissum bright yellow. This pattern is found *inter alia* in *Myiodynastes hemichrysus*, *Megarhynchus pitangua*, *Conopias parvus*, *Myiozetetes cayanensis* and *similis*, and *Pitangus sulphuratus* and *lictor*.

In Table II the species of these genera are listed with some of the character states used to separate them. The table shows the species in each genus are for the most part more closely related to each other than they are to any outside species; what is not clear is how many genera should be recognized. *Myiodynastes* is separated from all others except *Megarhynchus* by large size, long stout bill and short tarsus (except for *bairdii*), and from all except *Conopias parvus* by its hole-nesting habits. In external form *Megarhynchus* is merely an exaggerated *Myiodynastes* with a long, deep, decurved bill, but it does make an exposed, cup-shaped nest high up in trees, a typical *Tyrannus*-type nest, in contrast to the hole nesters. Fitzpatrick (*in litt.*) says *Megarhynchus* is much closer to *Pitangus* in behavior, since it feeds in the open, rather than within the foliage as does *Myiodynastes*. The three typical *Myiozetetes*, *cayannensis*, *granadensis* and *similis*, are well defined by short bill, globular nest and syrinx unlike any other; the nest of *luteiventris* [placed in *Tyrannopsis* by Zimmer (*Ms.*), and Meyer de Schauensee (1966)] is unknown. However, they share the short bill with *Conopias inornatus* (nest cup-shaped), and the globular nest with *Pitangus sulphuratus* (large and long-billed). *Conopias* is the least known genus as far as behavioral or anatomical characters go. *C. parva* is a hole nester; if this holds for the other two "typical" species, then *Conopias* is probably more closely related to *Myiodynastes* than to *Myiozetetes*. *C. inornatus* has the size and proportions of *Myiozetetes*, but lacks a brightly colored crest, as do *Conopias trivirgata* and *chinchoneti* for the most part, and has yellow

TABLE 2.

Species of Tyranninae	Av. wing length	Bill as % of wing	Tarsus as % of wing	Crest: + present 0 absent	Nest type	Syrinx from Ames	Cranium from Warter
Myiodynastes luteiventris	117	22.1	17.0	+	hole in tree	*Tyrannus* group	typical tyrannine
maculatus	112	24.0	17.8	+	hole or niche	not examined	typical tyrannine
bairdii	119	25.7	21.8	+	hole or niche	*Tyrannus* group	not examined
hemichrysus	107	23.8	17.9	+	niche	not examined	not examined
chrysocephalus	112	24.0	17.0	+	niche	not examined	not examined
Conopias trivirgata	75	22.8	23.4	trace	unknown	*Tyrannus* group	not examined
cinchoneti	86	22.4	20.0	trace	unknown	not examined	not examined
parva	82	25.1	21.0	+	hole or old nest	not examined	not examined
inornata	96	18.4	21.6	0	neat, shallow cup	not examined	not examined
Myiozetetes luteiventris	80	17.5	19.4	+	unknown	not examined	not examined
cayannensis	89	18.1	21.4	+	globular	ungrouped	typical tyrannine
granadensis	92	17.3	19.5	+	globular	ungrouped	typical tyrannine
similis	89	18.5	21.2	+	globular	ungrouped	typical tyrannine
Megarhynchus pitangua	121	28.8	16.6	+	shallow cup	*Tyrannus* group	typical tyrannine
Pitangus sulphuratus	110	25.6	22.2	+	globular	*Tyrannus* group	typical tyrannine, but *lictor* differs from *sulphuratus* more than any other congeners
lictor	91	26.9	21.4	+	cup	ungrouped	

rather than buff inner edges to the primaries. Based on one record (Cherrie, 1916: 238), *inornatus* builds a neat shallow cup nest, covered with lichens, and saddled on a large limb. If true, this sets *inornatus* apart from either *Conopias* or *Myiozetetes.* For the moment I leave *inornatus* in *Conopias*, although Zimmer (*Ms.*) and Meyer de Schauensee (1966) place it in *Myiozetetes.* A final problem in this group is the status of the two *Pitangus* species, *sulphuratus* and *lictor.* The two are virtually identical in plumage and proportions, and have more slender bills than other tyrannines. However, *sulphuratus* builds a globular nest, and *lictor* an open cup (Haverschmidt, 1957: 240; Smith, 1962: 111); the eggs of *lictor* are a much broader oval than those of *sulphuratus* (Meise, 1968: 78); *sulphuratus* has a typical tyrannine syrinx, but according to Ames (1971: 159),"*Pitangus lictor* lacks most of the features of the [*Tyrannus*] group and, in view of the structural homogeneity among those listed above, it is difficult to believe *lictor* and *sulphuratus* are more closely related to each other than the latter is to *Tyrannus*"; and Warter (1965: 36) says the crania of *lictor* and *sulphuratus* differ more than any other congeners . If *lictor* and *sulphuratus* are not congeneric, there is no logical genus in which to place the former. With its slender bill, it is the antithesis of the other cup-nest maker *Megarhynchus*, and on syringeal characters it differs as much from *Myiodynastes*, *Megarhynchus* and *Conopias* as it does from *P. sulphuratus. Myiozetetes* also differs from the tyrannines on syringeal characters, but not in the same way as *lictor*, and the nest of the latter is unlike the globular nest of *Myiozetetes.* Wetmore (1972: 422) says *lictor* should probably be placed in a separate genus, but considering my imperfect knowledge of this and related groups, I cannot see creating a new genus at this time. I shall leave *lictor* in *Pitangus*, but only for lack of a better place to put it.

I recognize the above five genera, not because I consider them satisfactory, but because at the moment I have nothing better to suggest. A case can be made for uniting *Myiozetetes* with *Conopias*, or *Pitangus* with *Myiozetetes*, but as noted in the discussion above, there are good reasons for not doing so. Until more is known about the behavior and nesting habits of some of the more obscure species, I feel more comfortable leaving them as they are. They are listed in the order *Pitangus*, *Megarhynchus*, *Myiozetetes*, *Conopias* and *Myiodynastes.*

Legatus leucophaius is almost identical in both juvenal and adult plumages with *Empidonomus varius*; the only noticeable difference is the pale buff edge on the inner webs of the primaries in *leucophaius* contrasted with the yellow edge in *varius.* In size, however, *leucophaius* is smaller, with a proportionately shorter, broader bill, shorter tail but longer tarsus. They differ markedly in nesting habits, *leucophaius* usurping the domed nests of other species, while *varius* builds an open cup. Warter (1965: 32) found *Legatus* had a type 2 nasal septum like *Myiarchus*, rather than the type 1 found in the rest of the restricted tyrannines, and Ames (1971: 159) reported the syrinx to be unlike the rest of the *Tyrannus* group. Considering these differences, the similarity in plumage is probably due to convergence.

Empidonomus varius and *aurantioatrocristatus* are closely related to *Tyrannus.* They are an obvious species pair, being almost identical in measurements, and each having a long blackish crest with bright yellow vertex; *varius*, however, is streaked above and below, while *aurantioatrocristatus* is plain brown above and gray below. Meise (1949: 71) considered *Empidonomus* separable from *Tyrannus* by its short bill and long tail. The former does have a short bill compared to the Tropical Kingbird, *T. melancholicus*, but no shorter than the North American Kingbird, *T. tyrannus*, the bill/wing ratios being 17–18 per cent. Similarly, the tails of *Empidonomus* species are proportionately the same as that of *T.*

melancholicus, 81–83 per cent of wing length. Syrinx, cranium, notching of primaries, and nest form are the same in both genera. Further evidence of the close relationship of *Empidonomus* and *Tyrannus* is the fact, demonstrated by Meise (1949: 61) that *Laphyctes apolites* Cabanis and Heine is a hybrid between *E. varius* and *T. melancholicus.* The one character I consider sufficient to maintain their separation is the much more slender build of *Empidonomus.* When specimens of the two genera, prepared by the same collector, are compared, those of *Empidonomus* are invariably more slender and cigar-shaped, while those of *Tyrannus* are broader and more chesty. While such a difference is not precise, it must reflect some anatomical and probably behavioral difference, and for the moment I recognize the two genera. The streaked plumage of *varius* would also be out of place in *Tyrannus.*

Tyrannopsis is a peculiar monotypic genus that is apparently most closely related to *Tyrannus*, although the single species *sulphurea* was for a long time carried in *Myiozetetes*. It differs from *Myiozetetes* in being larger, with a proportionately shorter tail and longer culmen, in having a syrinx belonging to the *Tyrannus* group, while that of *Myiozetetes* is unlike any other, and in building a *Tyrannus*-like cup-shaped nest instead of a globular one. In plumage, *sulphuraea* is a saturated version of *Tyrannus melancholicus* with a dark gray head and orange crest, dark olive back, gray throat with a white center, and yellow breast and belly. Where the gray of the sides of the throat bleeds into the yellow breast, there is olive streaking, a character not found in any of the kingbirds. In size and proportions *Tyrannopsis* fits within the overall limits of *Tyrannus*, but is not close to any one species, having the short bill of the North American *tyrannus* and *verticalis*, and the long tarsus of the insular *caudifasciatus.* The male lacks the notched primaries present in all continental *Tyrannus.* The range of *sulphurea* is extensive in the tropical lowlands east of the Andes, south to southern Amazonia and east to Maranhão, Brasil, but its distribution is restricted to areas where the Mauritia palm, in which it nests, is found. Meise (1949: 71) placed *sulphurea* in *Tyrannus*, but Smith (1966) in his review of that genus did not mention it as a possible *Tyrannus.* To further complicate its possible relationships, Zimmer (*Ms.*) followed by Meyer de Schauensee (1966: 346) added to *Tyrannopsis Myiozetetes luteiventris*, a species that by no stretch of the imagination could be considered a *Tyrannus. Luteiventris* is a miniature of *sulphurea* in coloration, even smaller than the smallest *Myiozetetes*, and it is identical with the latter in proportions; its nest is not known. I feel, as did Blake (1961), that *luteiventris* should remain in *Myiozetetes.* I also recognize *Tyrannopsis* as a genus, at least until it is better known behaviorally.

The last genus in the family is *Tyrannus.* It is the most widespread geographically, both as a genus and in the individual ranges of some species, and the species are usually aggressive and dominant wherever they occur. Considering the uniformity of the species, both morphologically and behaviorally, they probably represent the most recent radiation in the family.

Smith (1966) comprehensively reviewed communications and relationships within the genus *Tyrannus.* He merged with *Tyrannus* the monotypic *Tolmarchus* of the West Indies, and *Muscivora* with its two fork-tailed species, *tyrannus* and *forficata.* The merging of *Tolmarchus* with *Tyrannus* had been previously recommended by Meise (1949: 73) and Bond (1958); it is supported by syringeal and cranial evidence. Smith's merging of *Muscivora* has had a mixed reception, being followed by Lanyon (1967a: 606) and by Mayr and Short (1970: 59), but opposed by Howell (1972: 325). The union of *Tyrannus* with *Muscivora* requires that *Muscivora tyrannus* be called *Tyrannus savana*, to avoid homonymy with the North American *Ty-*

rannus tyrannus. Smith's decision was based on behavioral considerations, but other evidence is equally strong. Cranial characters, syrinx, nest form and notched primaries are alike in *Muscivora* and *Tyrannus*. Except for the long, forked tail, the *Muscivora* species are almost identical in size and proportions with the North American *Tyrannus tyrannus* and *verticalis*. This is of particular interest, since Meise (1949: 75) believed *savana* and *forficata* evolved independently from *T. tyrannus* and *verticalis* respectively. Further evidence of close relationship is found in the hybrid between *verticalis* and *forficata* described by Davis and Webster (1970). If *savana* and *forficata* did evolve independently, then their long forked tails are convergent, and there is no taxon *Muscivora*. At present I do not know of any characters that could be used to prove or disprove this hypothesis. I do not recognize *Muscivora* even as a subgenus because of its close relation to *Tyrannus*, but I keep *savana* and *forficata* together because of their possible common origin.

PHYLOGENY

Any attempt to derive a phylogeny requires some knowledge of the primitive and derived states of the characters on which the classification is based. Also, it must be possible to determine whether the derived state is monophyletic or whether it evolved independently two or more times, and as a corollary, whether a state is really primitive or just a secondary regression from a derived state. When the characters used to classify the Tyrannidae are viewed in this light, there are few that serve for determining a phylogeny.

There are a number of morphological characters that occur regularly in the family, but the characters are so randomly distributed they must have evolved or been lost independently many times. Bright coronal crests, aberrant primaries, and holaspidean, taxaspidean or pycnaspidean tarsi are found in unrelated groups in all three subfamilies, and merely represent a genetic potential within the family for this type of mutation. Even the pendent, pyriform nest, which is an elaborate structure requiring a special set of behavioral patterns for its construction, must have evolved at least twice—in the *Myiobius* group of the Fluvicolinae and in the tody-tyrants of the Elaeniinae. As Ames (1971: 150) noted, "The application of syringeal morphology increases in reliability toward the generic level," and he made no attempt to rate his groups of genera as primitive or advanced. The only characters that seem amenable to classification as primitive or derived are the cranial characters of Warter.

In classifying the states of the cranial characters, I have used the evidence of their present distribution within the subfamilies, rather than trying to determine which are intrinsically primitive or derived.

1) Nasal septum – types 1 and 2 are found in significant proportions in both Tyranninae and Elaeniinae, while a type 6 septum is found in all the Fluvicolinae except the two aberrant genera *Muscigralla* and *Onychorhynchus*. Types 3 and 5 occur once each in the Fluvicolinae and occasionally in the Elaeniinae. Type 1 or 2 is almost certainly primitive, and the others derived, but only type 6 appears significant phylogenetically.
2) Interorbital septum – type 1 occurs regularly in the Fluvicolinae, exclusively in the Tyranninae and twice in the Elaeniinae. Type 2 is mostly confined to the Fluvicolinae, but occurs twice in the Elaeniinae; type 3 is found occasionally in both, but type 4 is found only in the Elaeniinae, where it occurs in 77 per cent of the studied genera. Evidently type 1 is the primitive type, type 4 is derived and characterizes the Elaeniinae, and types 2 and 3 have evolved

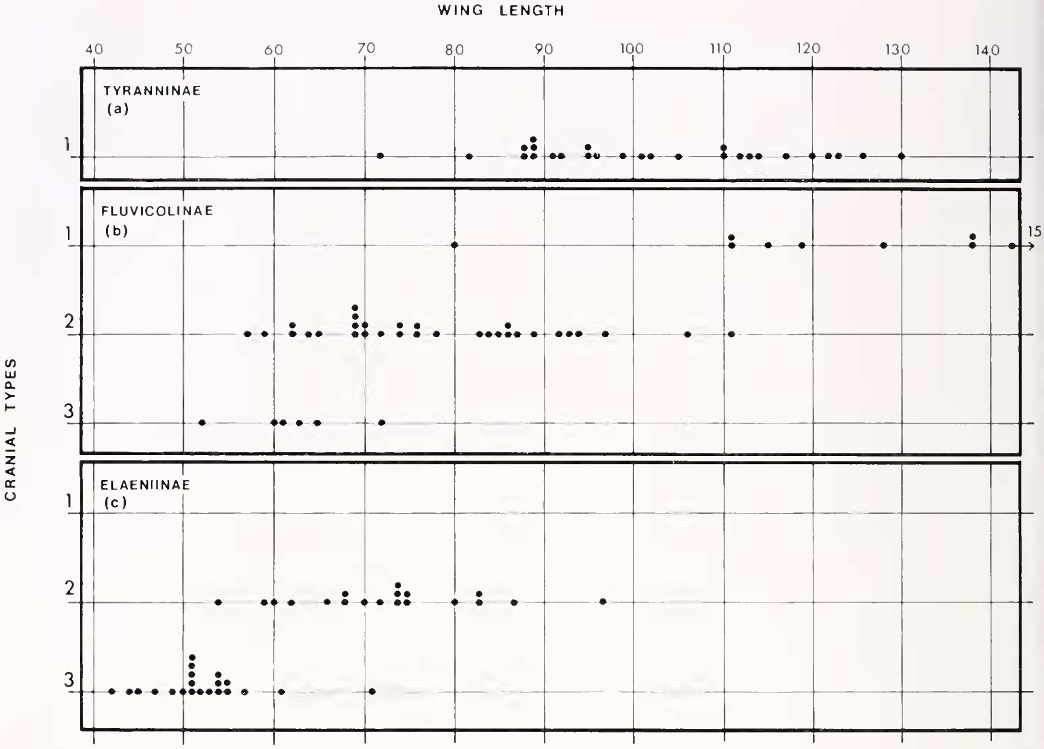

Figure 6. Warter's cranial types plotted as a function of wing length for the three subfamilies of Tyrannidae. In the Tyranninae (a) only type 1 occurs, and it is characteristic of the subfamily. In the Fluvicolinae (b) and Elaeniinae (c), the cranial types show a close correlation with size, as represented by wing length, and are without taxonomic significance.

independently in Fluvicolinae and Elaeniinae.

3) Palatines – type 1 occurs regularly in all three subfamilies, and is the only type found in the Tyranninae; it must be the primitive type. Type 2 is also common in the Fluvicolinae and Elaeniinae, but type 3 is confined with one exception to the "Contopine" lineage of the Fluvicolinae.

4) Cranium – with the exception of the Tyranninae, the cranial types are strongly correlated with size as expressed by wing length—type 1 being found in the largest birds and type 3 in the smallest (Fig. 6). In the Tyranninae only type 1 occurs, regardless of wing length. Assuming the primitive flycatchers were small arboreal forms, nearest the present Elaeniinae, then types 2 and 3 are primitive, and type 1 derived.

Figure 7 is a diagram suggesting the possible origin of the subfamilies of flycatchers, incorporating the primitive and derived states of the cranial characters. The putative proto-flycatcher appears within the circle, with the different subfamilies leading off from it. The derived cranial characters defining the subfamilies are indicated, and in two cases the subfamilies are further subdivided. Finally, Ames' seven syringeal groups are indicated, showing the close correlation between the two

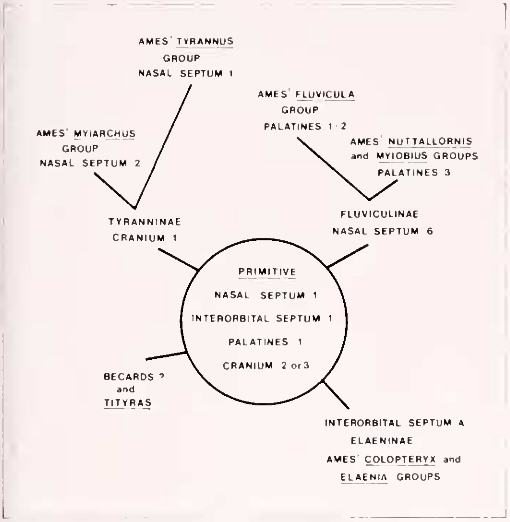

Figure 7. Postulated origin of the subfamilies of Tyrannidae, based on Warter's cranial characters. Ames' groups of genera, based upon syringeal characters, are added to show the close correlation between these character complexes.

types of anatomical characters. It is tempting to try to carry out further subdivisions within the subfamilies, based on cranial or other evidence, but it is unprofitable for two reasons. First, the evidence, even within the cranial characters, becomes conflicting, and second, there are too many unexamined genera whose allocation would be guesswork.

The circular form of diagram in Figure 7 is used because the three subfamilies of flycatchers seem to have arisen independently rather than sequentially, one from another. There are no genera in any given subfamily that seem ancestral to or even closely related to either of the other subfamilies. *Onychorhynchus* was placed in my Elaeniinae by Warter, and in the Fluvicolinae here, but the difficulty is not that *Onychorhynchus* is intermediate between the two, but that its high specialization makes it difficult to place it in either. If my reconstruction of the proto-flycatcher characters is correct, then none of the modern taxa retain the primitive condition.

Elaeniinae—This subfamily is characterized by the type 4 interorbital septum, which is found in 27 of the 35 genera examined by Warter. The remaining genera have variously types 1, 2 or 3, and the evidence suggests these represent a secondary loss of type 4 rather than the retention of a primitive state. Seven of these genera—*Myiopagis*, *Elaenia*, *Suiriri*, *Sublegatus*, *Phaeomyias*, *Zimmerius* and *Tyrannulus*—belong to the old restricted subfamily Elaeniinae, and all but *Sublegatus* and *Zimmerius* are part of Ames' *Elaenia* syringeal group. However, their relationships are otherwise divided among groups still retaining the type 4 interorbital septum. *Elaenia*, *Suiriri* and *Sublegatus* share a type 5 nasal septum with the nearly related *Anairetes*, *Serpophaga*, *Inezia* and *Mecocerculus*. This type of septum is certainly derived and is found only here, with the exception of the peculiar *Muscigralla* of the Fluvicolinae. *Phaeomyias*, on the other hand, is most closely related to *Camptostoma*, which has a type 4 interorbital septum. The last genus to lack the type 4 interorbital septum is *Polystictus*, which is related to *Pseudocolopteryx*, which has the normal type. A second of Ames' syringeal groups, the *Colopteryx* group, includes most of the tody-tyrants, all of which have the type 4 interorbital septum.

Fluvicolinae—The Fluvicolinae are characterized by the type 6 nasal septum, which is found in all genera except the highly specialized *Muscigralla* and *Onychorhynchus*. This type of nasal septum has also evolved independently twice in the Elaeniinae, in *Polystictus* and in *Zimmerius*. The fact that these two genera have the Fluvicoline nasal septum and lack the characteristic type 4 interorbital septum of the Elaeniinae might suggest that one or both are primitive links between the Elaeniinae and Fluvicolinae. However, in general conformation and appearance they are typically Elaeniinae and unlike any Fluvicolinae, so I believe the resemblance in cranial characters is due to convergence. Certainly it would be difficult to conceive of both representing the same primitive stock, since *Polystictus* is a brown, streaked grassland form, and *Zimmerius* a green, forest group.

The Fluvicolinae are further subdivided by the possession of the derived type 3 palatine in Warter's "Contopine" lineage. This palatine occurs elsewhere only in *Platyrinchus* of the Elaeniinae, where it is almost certainly independently derived. Three of the genera of the "Contopines," *Nuttallornis*, *Cnemotriccus* and *Myiophobus*, have a type 2 palatine, but this almost certainly represents a secondary loss of the type 3. This is most evident for *Nuttallornis*, whose congeners in *Contopus* all have type 3 palatines, and for *Cnemotriccus*, whose closest relative is *Empidonax* with type 3 palatines. *Myiophobus* does not have any single close relative, but the genera closest to it on other characters, *Mitrephanes*, *Pyrrhomyias* and *Myiobius*, all have type 3 palatines.

Ames' syringeal groups support this derivation of the Fluvicolinae. Two of them, the *Myiobius* group and the *Nuttallornis* group, are part of the "Contopine" lineage, while the *Fluvicola* group falls in the restricted Fluvicolines.

Tyranninae—The Tyranninae are remarkable in that all genera, with the exception of *Attila*, have one of two invariant sets of cranial characters. All but *Attila* have type 1 interorbital septa, palatines and crania, and these are associated with either type 1 or 2 nasal septa. The restricted Tyrannines all have type 1 nasal septa, with the exception of *Legatus*, and the Myiarchine group have type 2, with the exception of *Attila*. The latter type is presumably the derived form, since the type 1 is more common among the Elaeniinae. Ames' syringeal groups fit this dichotomy of the Tyranninae. The *Myiarchus* group includes those genera with type 2 nasal septa, plus *Attila*, and the *Tyrannus* group includes only genera with type 1 nasal septa, the restricted Tyranninae.

The most interesting aspect of the Tyrannine cranium is the extreme uniformity, as if all the character states were inherited as a package. This is not implicit in the type 1 characters as such: type 1 interorbital septa occur with all three types of palatines and crania in the Elaeniinae and Fluvicolinae, and type 1 palatines occur with all types of interorbital septa and cranial types. The only correlation that appears structural is that type 1 crania almost always occur with type 1 palatines; the reverse, however, is not true. The uniformity in the Tyrannine cranium suggests a late origin for this subfamily; the fact that they are a highly successful and dominant group with evidence of recent radiation supports this view. On the other hand, three of the character states delineating this uniform cranium are primitive; only the type 1 cranium is a derived state. This leaves us with the anomaly of the most successful subfamily being the most primitive anatomically. Possibly the explanation is that retention of the primitive or generalized characters left the Tyranninae with a greater potential for radiation, which they have only recently exploited.

SUMMARY

A new classification of the Tyrannidae is presented, based on available morphological, anatomical, behavioral and distributional data. The most useful recent studies on the higher classification of the Tyrannidae were those of Warter (1965) on the cranial characters of the Tyrannoidea, and Ames (1971) on the syrinx of the Passeriformes. The family includes all those genera accepted by Hellmayr (1927), five genera formerly included in the Cotingidae —*Attila*, *Pseudattila*, *Casiornis*, *Laniocera* and *Rhytipterna*—and *Corythopis* from the former family Conopophagidae.

The seven subfamilies of Hellmayr, Fluvicolinae, Tyranninae, Myiarchinae, Platyrinchinae, Euscarthminae, Serpophaginae and Elaeniinae, are reduced to three. The Fluvicolinae now include that part of the Myiarchinae including the genera *Nuttallornis* through *Onychorhyn-*

chus, and the remainder of the Myiarchinae plus the former Cotingid genera are placed in the Tyranninae. The other four subfamilies are merged into one, for which Elaeniinae is the oldest name. The subfamilies are listed in the order Elaeniinae, Fluvicolinae, Tyranninae, since this seems to represent the progression from most primitive or generalized to most specialized or successful.

The genera are listed within each subfamily also from generalized to specialized. However, these are such subjective decisions that the order of Hellmayr (in reverse) is not disturbed unless there is positive evidence for making a change. There has been little analysis of the genera of flycatchers over the past century, and for the most part they have been accepted uncritically from checklist to checklist. Thirty-six of Hellmayr's genera are here synonymized, one is resurrected and one new genus is described. The latter is *Zimmerius*, created for five species formerly in the genus *Tyranniscus*. The new classification is summarized in Appendix A.

REFERENCES

American Ornithologists' Union. 1957. Check-list of North American birds, 5th edition. Baltimore: American Ornithologists' Union. xiii + 691 pp.

American Ornithologists' Union, Checklist Committee. 1947. Twenty-second supplement to the American Ornithologists' Union Check-list of North American birds. Auk **64:** 445–452.

Ames, P. L. 1971. The morphology of the syrinx in Passerine birds. Bull. Peabody Mus. Nat. Hist. **37:** 194 pp.

———, M. A. Heimerdinger and S. L. Warter. 1968. The anatomy and systematic position of the Ant pipits *Conopophaga* and *Corythopis*. Postilla (Yale) No. 114: 32 pp.

Berlepsch, H. Graf von. 1907. Studien über Tyranniden. Ornis **14:** 463–493.

Blake, E. R. 1961. Variation in *Myiozetetes luteiventris*. Fieldiana: Zool. **44:** 63–66.

Bond, J. 1943. Nidification of the Passerine birds of Hispaniola. Wilson Bull. **55:** 115–125.

———. 1958. Third supplement to the Check-list of Birds of the West Indies (1956). Acad. Nat. Sci. Philadelphia. 11 pp.

Burmeister, H. 1869. Contributions to the ornithology of the Argentine Republic and adjacent lands. Proc. Zool. Soc. London, 1868: 633–636.

Cabanis, J. 1892. Sitzungs-Bericht für 1891, Deutsch. Orn. Gesell. Berlin; Bericht. über die November-Sitzung. Journ. f. Orn. **40:** 123–129.

Cabanis, J. L. and F. Heine. 1959. Verzeichniss der Ornithologischen Sammlung des Oberamtmann Ferdinand Heine, pt. II. Halberstadt. 175 pp.

Cherrie, G. K. 1916. A contribution to the Ornithology of the Orinoco region. Mus. Brooklyn Inst. Arts Sci., Sci. Bull. **2:** 133–374.

Davis, L. I. and F. S. Webster, Jr. 1970. An intergeneric hybrid flycatcher (*Tyrannus* × *Muscivora*). Condor **72:** 37–42.

Dickey, D. R. and A. J. van Rossem. 1938. The birds of El Salvador. Field Mus. Nat. Hist., Zool Ser. **23:** 609 pp.

Dorst, J. 1957. Description d'une espèce nouvelle de Tyran du genre *Serpophaga* du Pérou septentrional. Bull. Mus. Nat. Hist. Nat., Paris (2) **29:** 207–209.

Euler, C. 1900. Descripção de ninhos e ovos das aves do Brazil. Rev. Mus. Paulista **4:** 9–148.

Fitzpatrick, J. W. 1976. Systematics and biogeography of the Tyrannid genus *Todirostrum* and related genera (Aves). Bull. Mus. Comp. Zool. **147:** 435–463.

Griscom, L. 1929. A collection of birds from Cana, Darien. Bull. Mus. Comp. Zool. **69:** 149–190.

Haverschmidt, F. 1957. The nest of *Pitangus lictor* and *Coryphotriccus parvus*. Auk **74:** 240–242.

———. 1968. Birds of Surinam. Edinburgh: Oliver and Boyd. xvi + 455 pp.

———. 1973. White-ringed Flycatcher nest-building in old nest of the Yellow-rumped Cacique. Auk **90:** 207–208.

Hellmayr, C. E. 1927. Catalogue of Birds of the Americas and the adjacent islands, Part V, Tyrannidae. Field Mus. Nat. Hist., Zool. Ser. **13:** vi + 517 pp.

Howell, T. R. 1972. Birds of the lowland pine savanna of northeastern Nicaragua. Condor **74:** 316–340.

Ihering, H. von. 1904. The biology of the Tyrannidae with respect to their systematic arrangement. Auk **21:** 313–322.

Lanyon, W. E. 1967a. Review: Communications and relationships in the genus *Tyrannus*. Auk **84:** 606–609.

———. 1967b. Revision and probable evolution of the *Myiarchus* flycatchers of the West Indies. Bull. Amer. Mus. Nat. Hist., **136:** 329–370.

Mayr, E. 1971. New species of birds described from 1956 to 1965. Journ. f. Orn. **112:** 302–316.

——— and D. Amadon. 1951. A classification of recent birds. Amer. Mus. Novit. No. 1496, 42 pp.

——— and L. L. Short. 1970. Species taxa of North American birds. Publ. Nuttall Orn. Club No. 9, 127 pp.

Meise, W. 1949. Über einen Gattungsbastard und eine Zwillingsart der Tyrannen nebst Bemerkungen über Zugweite und Flügelform; in Ornithologie als biologische Wissenschaft, pp. 61–83. Mayr, E. and E. Schütz, eds. Heidelberg: Carl Winter Universitätsverlag.

———. 1968. *In* Schönwetter's Handbuch der Oologie. Lief. **15:** 65–128. Berlin: Akad.-Verlag.

Meyer de Schauensee, R. 1966. The Species of birds of South America with their distribution. Acad. Nat. Sci. Phila. Distributed by Livingston Pub. Co. Narberth. xvii + 577 pp.

———. 1970. A guide to the birds of South America. Acad. Nat. Sci. Philadelphia. Distributed by Livingston Publ. Co.: Wynnewood. xvi + 470 pp.

Monroe, B. L. 1975. Taxonomic significance of wing movements in certain Tyrannids and Mimids. Paper delivered at A.O.U. meeting, Winnipeg, Manitoba.

Parkes, K. C. 1973. Distribution and generic placement of the Plain Tyrannulet (*Inezia inornata*). Condor **75:** 249–250.

Peters, J. L. 1931–. Check-list of the birds of the world, vols. 1–15 (8 and 11 not yet published). Cambridge, Massachusetts: Mus. Comparative Zoology.

——— and J. A. Griswold, Jr. 1943. Birds of the Harvard Peruvian expedition. Bull. Mus. Comp. Zool. **92:** 281–327.

Phillips, A., J. Marshall and G. Monson. 1964. The birds of Arizona. Tucson: Univ. Arizona Press. xviii + 212 pp.

Plótnick, R. and M. J. I. Pergolani de Costa. 1955. Clave de las familias de Passeriformes representadas in Argentina. Rev. Invest. Agric. (Buenos Aires) **9:** 65–88.

Ridgway, R. 1891. Note on *Pachyramphus albinucha*, Burmeister. Proc. U.S. Nat. Mus. **14:** 479–480.

———. 1907. The Birds of North and Middle America, pt. IV. Bull. U.S. Nat. Mus. **50**, pt. IV: 973 pp.

Sclater, P. L. 1888. Catalogue of Birds in the British Museum, vol. 14. London: British Museum (Nat. Hist.). xx + 494 pp.

———. 1893. Remarks on a rare Argentine bird. Proc. Zool. Soc. London, 1893: 166–168, pl. 7.

Short, L. L. Jr. 1975. A zoogeographic analysis of the South American Chaco avifauna. Bull. Amer. Mus. Nat. Hist. **154:** 163–352.

——— and T. D. Burleigh. 1965. An intergeneric hybrid flycatcher (*Contopus* × *Empidonax*) from Idaho. Proc. Biol. Soc. Washington **78:** 33–37.

Skutch, A. F. 1960. Life Histories of Central American birds, Pt. II. Pacific Coast Avifauna, No. 34, 591 pp.

Slud, P. 1967. The birds of Cocos Island [Costa Rica]. Bull. Amer. Mus. Nat. Hist. **134:** 261–296.

Smith, W. J. 1962. The nest of *Pitangus lictor.* Auk **79:** 108–111.

———. 1966. Communications and relationships in the genus *Tyrannus.* Publ. Nuttall Orn. Club, No. 6, 250 pp.

———. 1971. Behavioral characteristics of Serpophaginine Tyrannids. Condor **73:** 259–286.

——— and F. Vuilleumier. 1971. Evolutionary relationships of some South American ground tyrants. Bull. Mus. Comp. Zool. **141:** 179–268.

Smithe, F. B. 1966. The birds of Tikal. New York: Natural History Press. 350 pp., 39 pl.

Snethlage, E. 1935. Beiträge zur Fortpflanzungs-biologie brasilianischer Vögel. Journ. f. Orn. **83:** 532–562.

Snow, D. W. 1973. The classification of the Cotingidae (Aves). Breviora, Mus. Comp. Zool., 409: 27 pp.

———. 1975. The classification of the manakins. Bull. Brit. Orn. Club **95:** 20–27.

Swarth, H. S. 1931. The avifauna of the Galapagos Islands. Occ. Pap. Cal. Acad. Sci., No. 18, 299 pp.

Townsend, C. H. 1895. Birds from Cocos and Malpelo Islands, with notes on petrels obtained at sea. Bull. Mus. Comp. Zool., **27:** 121–126.

Warter, S. L. 1965. The cranial osteology of the New World Tyrannoidea and its taxonomic implications. Ph.D. thesis, Louisiana State University. Available from Xerox University Microfilms, Ann Arbor, Michigan.

Webster, J. D. 1968. A revision of the Tufted Flycatchers of the genus *Mitrephanes.* Auk **85:** 287–303.

Wetmore, A. 1960. A classification for the birds of the world. Smiths. Misc. Coll. **139** (11): 37 pp.

———. 1972. The birds of the Republic of Panama, Pt. 3. Smiths. Misc. Coll., **150**, pt. 3: 631 pp.

Zimmer, J. T. 1936. Studies of Peruvian Birds, 23. Notes on *Doliornis, Pipreola, Attila, Laniocera, Rhytipterna,* and *Lipaugus.* Amer. Mus. Novit., No. 893, 15 pp.

———. 1937a. Studies of Peruvian Birds, No. 26. Notes on the Genera *Agriornis, Muscisaxicola, Myiotheretes, Ochthoeca, Colonia, Knipolegus, Phaeotriccus, Fluvicola,* and *Ramphotrigon.* Amer. Mus. Novit., No. 930, 27 pp.

———. 1937b. Studies of Peruvian Birds, No. 27. Notes on the Genera *Muscivora, Tyrannus, Empidonomus,* and *Sirystes,* with further notes on *Knipolegus.* Amer. Mus. Novit., No. 962, 28 pp.

———. 1937c. Studies of Peruvian Birds, No. 28. Notes on the Genera *Myiodynastes, Conopias, Myiozetetes,* and *Pitangus.* Amer. Mus. Novit., No. 963, 28 pp.

———. 1938. Studies of Peruvian Birds, No. 29. The Genera *Myiarchus, Mitrephanes,* and *Cnemotriccus.* Amer. Mus. Novit., No. 994, 32 pp.

———. 1939a. Studies of Peruvian Birds, No. 30. Notes on the Genera *Contopus, Empidonax, Terenotriccus* and *Myiobius.* Amer. Mus. Novit., No. 1042, 13 pp.

———. 1939b. Studies of Peruvian Birds, No. 31. Notes on the Genera *Myiotriccus, Pyrrhomyias, Myiophobus, Onychorhynchus, Platyrinchus, Cnipodectes, Sayornis,* and *Nuttallornis.* Amer. Mus. Novit. No. 1043, 15 pp.

———. 1939c. Studies of Peruvian Birds, No. 33. The Genera *Tolmomyias* and *Rhynchocyclus* with further notes on *Ramphotrigon.* Amer. Mus. Novit., No. 1045, 23 pp.

———. 1940a. Studies of Peruvian Birds, No. 34. The Genera *Todirostrum, Euscarthmornis, Snethlagea, Poecilotriccus, Lophotriccus, Myiornis, Pseudotriccus,* and *Hemitriccus.* Amer. Mus. Novit., No. 1066, 23 pp.

———. 1940b. Studies of Peruvian Birds, No. 35. Notes on the Genera *Phylloscartes, Euscarthmus, Pseudocolopteryx, Tachuris, Spizitornis, Yanacea, Uromyias, Stigmatura, Serpophaga,* and *Mecocerculus.* Amer. Mus. Novit., No. 1095, 19 pp.

———. 1941a. Studies of Peruvian Birds, No. 36. The Genera *Elaenia* and *Myiopagis.* Amer. Mus. Novit., No. 1108, 23 pp.

———. 1941b. Studies of Peruvian Birds, No. 37. The Genera *Sublegatus, Phaeomyias, Camptostoma, Xanthomyias, Phyllomyias,* and *Tyranniscus.* Amer. Mus. Novit., No. 1109, 25 pp.

———. 1941c. Studies of Peruvian Birds, No. 38. The Genera *Oreotriccus, Tyrannulus, Acrochordopus, Ornithion, Leptopogon, Mionectes, Pipromorpha* and *Pyrocephalus.* Amer. Mus. Novit., No. 1126, 25 pp.

———. 1955. Further notes on Tyrant Flycatchers (Tyrannidae). Amer. Mus. Novit., No. 1749, 24 pp.

APPENDIX A

Sequence of Genera with Synonyms

Elaeniinae

- *Phyllomyias* (syn: *Xanthomyias, Oreotriccus, Acrochordopus,* and *Tyranniscus nigrocapillus, uropygialis* and *cinereiceps*)
- *Zimmerius* (gen. nov. — includes "*Tyranniscus*" *bolivianus, vilissimus, cinereicapilla, gracilipes, viridiflavus*)
- *Ornithion* (syn: *Microtriccus*)
- *Camptostoma*
- *Phaeomyias*
- *Sublegatus*
- *Suiriri*
- *Tyrannulus*
- *Myiopagis*
- *Elaenia*
- *Mecocerculus*
- *Serpophaga*
- *Inezia*
- *Stigmatura*
- *Anairetes* (syn: *Uromyias, Yanacea*)
- *Tachuris*
- *Culicivora*
- *Polystictus*
- *Pseudocolopteryx*
- *Euscarthmus*
- *Mionectes* (syn: *Pipromorpha*)
- *Leptopogon*
- *Phylloscartes* (syn: *Pogonotriccus, Leptotriccus, Capsiempis*)
- *Pseudotriccus* (syn: *Caenotriccus*)
- *Corythopis*
- *Myiornis* (syn: *Perissotriccus*)
- *Lophotriccus* (syn: *Colopteryx*)
- *Atalotriccus*
- *Poecilotriccus* (syn: *Taeniotriccus*)
- *Oncostoma*
- *Hemitriccus* (syn: *Idioptilon, Euscarthmornis, Snethlagaea, Microcochlearius, Ceratotriccus*)
- *Todirostrum*
- *Cnipodectes*
- *Ramphotrigon*
- *Rhynchocyclus*
- *Tolmomyias*
- *Platyrinchus*

Fluvicolinae

- *Onychorhynchus*
- *Myiotriccus*
- *Terenotriccus*
- *Myiobius*
- *Myiophobus*
- *Aphanotriccus* (syn: *Praedo*)
- *Xenotriccus* (syn: *Aechmolophus*)
- *Pyrrhomyias*
- *Mitrephanes*

Contopus (syn: *Nuttallornis, Blacicus*)
Empidonax
Nesotriccus
Cnemotriccus
Sayornis
Pyrocephalus
Ochthoeca (syn: *Ochthornis, Colorhamphus*)
Myiotheretes (syn: *Cnemarchus, Ochthodiaeta*)
Xolmis (syn: *Pyrope*)
Neoxolmis
Agriornis
Muscisaxicola
Lessonia
Knipolegus (syn: *Phaeotriccus, Entotriccus, Eumyiobius*)
Hymenops
Fluvicola (syn: *Arundinicola*)
Colonia
Alectrurus (syn: *Yetapa*)
Gubernetes
Satrapa
Tumbezia
Muscigralla
Hirundinea
Machetornis
Muscipipra

Tyranninae

Attila (syn: *Pseudattila*)
Casiornis
Rhytipterna
Laniocera
Sirystes
Myiarchus (syn: *Hylonax, Eribates*)
Deltarhynchus
Pitangus
Megarhynchus
Myiozetetes
Conopias (syn: *Coryphotriccus*)
Myiodynastes
Legatus
Empidonomus
Tyrannopsis
Tyrannus (syn: *Muscivora, Tolmarchus*)

Sedis Incertae

Xenopsaris

APPENDIX B

Generic Changes Since Hellmayr (1927)

Acrochordopus = *Phyllomyias*, here synonymized

Aechmolophus Zimmer 1938, Auk **55**: 663 = *Xenotriccus*, Webster (1968: 289)

Alectrurus – includes *Yetapa*, Short (1975: 269)

Anairetes 1850, replaces *Spizitornis* 1920; Peters and Griswold (1943: 316); includes *Yanacea* and *Uromyias*, which see

Aphanotriccus – includes *Praedo*, Griscom (1929: 176)

Arundinicola = *Fluvicola*, here synonymized

Attila – transferred from the Cotingidae, Snow (1973: 7); Ames (1971: 155)

Blacicus = *Contopus*, Bond (1943: 117)

Cnemotriccus = *Pseudotriccus*, Zimmer (1940a: 22)

Capsiempis = *Phylloscartes*, here synonymized

Casiornis – transferred from the Cotingidae, Snow (1973: 7); Ames (1971: 155)

Ceratotriccus = *Idioptilon*, Fitzpatrick (1976); here synonymized with *Hemitriccus*

Cnemarchus = *Myiotheretes*, here synonymized; see also Smith and Vuilleumier (1971: 193)

Colopteryx = *Lophotriccus*, here synonymized

Colorhamphus = *Ochthoeca*, here synonymized

Conopias – includes *Coryphotriccus*, Meise (1949: 76)

Contopus 1855, replaces *Myiochanes* 1859, American Ornithologists' Union, Checklist Committee (1947: 449); includes *Nuttallornis* and *Blacicus*, which see

Corythopis – added to the Tyrannidae, Ames, Heimerdinger and Warter (1968)

Coryphotriccus = *Conopias*, Meise (1949: 76)

Elaenia – no longer includes *Myiopagis*, Zimmer (1941a: 20)

Entotriccus = *Knipolegus*, Short (1975: 270)

Eribates = *Myiarchus*, Swarth (1931: 84)

Eumyiobius Brodkorb 1937, Proc. Biol. Soc. Washington, **50**: 1 = *Knipolegus*, Zimmer, 1937b: 27

Euscarthmornis = *Idioptilon*, Zimmer (1940a: 13) = *Hemitriccus*, here synonymized

Fluvicola – includes *Arundinicola*, here united

Habrura 1859 = *Polystictus* 1850, Meyer de Schauensee (1966: 374)

Hemitriccus – includes *Ceratotriccus, Microcochlearius, Snethlagaea, Euscarthmornis* and *Idioptilon*, here united; see also Fitzpatrick (1976)

Hylonax = *Myiarchus*, Lanyon (1967b: 339)

Hymenops, 1828, replaces *Lichenops*, 1835, Meyer de Schauensee (1966: 342)

Idioptilon – includes *Euscarthmornis*, Zimmer (1940a: 13) = *Hemitriccus*, here synonymized

Knipolegus – includes *Phaeotriccus* and *Entotriccus*, Short (1975: 270)

Laniocera – transferred from the Cotingidae, Snow (1973: 7); Ames (1971: 155)

Leptotriccus = *Phylloscartes*, here synonymized

Lichenops 1835 = *Hymenops* 1828, Meyer de Schauensee (1966: 342)

Lophotriccus – includes *Colopteryx*, here united

Microcochlearius = *Idioptilon*, Fitzpatrick (1976) = *Hemitriccus*, here synonymized

Microtriccus = *Ornithion*, Zimmer (1941c: 3)

Mionectes – includes *Pipromorpha*, Dickey and van Rossem (1938: 397)

Muscivora = *Tyrannus*, Smith (1966: 167)

Myiarchus – includes *Hylonax* and *Eribates*, which see

Myiochanes 1859 = *Contopus* 1855, American Ornithologists' Union, Checklist Committee (1947: 449)

Myiopagis – synonymized in *Elaenia* by Hellmayr, but now recognized, Zimmer (1941a: 20)

Myiornis – includes *Perissotriccus*, Zimmer (1940a: 220)

Myiotheretes – includes *Cnemarchus* and *Ochthodiaeta*, here united; see also Smith and Vuilleumier (1971: 193)

Nuttallornis = *Contopus*, Phillips, Marshall and Monson (1964: 90)

Ochthodiaeta = *Myiotheretes*, here synonymized; see also Smith and Vuilleumier (1971: 193)

Ochthoeca – includes *Colorhamphus* and *Ochthornis*, here united

Ochthornis = *Ochthoeca*, here synonymized

Oreotriccus = *Phyllomyias*, here synonymized

Ornithion – includes *Microtriccus*, Zimmer (1941c: 3)

Perissotriccus = *Myiornis*, Zimmer (1940a: 22)

Phaeotriccus = *Knipolegus*, Short (1975: 270)

Phyllomyias – includes *Xanthomyias*, *Oreotriccus*, *Acrochordopus* and *Tyranniscus* (pt.), here united

Phylloscartes – includes *Pogonotriccus*, *Leptotriccus* and *Capsiempis*, here united

Pipromorpha = *Mionectes*, Dickey and van Rossem (1938: 397)

Pogonotriccus = *Phylloscartes*, here synonymized

Polystictus 1850, replaces *Habrura* 1859 – Meyer de Schauensee (1966: 374)

Praedo = *Aphanotriccus*, Griscom (1929: 176)

Pseudattila Zimmer 1936, Amer. Mus. Novit. No. 893: 6 = *Attila*, Short (1975: 265); transferred from the Cotingidae, Meyer de Schauensee (1970: 297), Snow (1973: 7)

Pseudotriccus – includes *Caenotriccus*, Zimmer (1940a: 22)

Pyrope = *Xolmis*; synonymized by Hellmayr (1927: 10), resurrected by Meyer de Schauensee (1966: 335), and synonymized again by Smith and Vuilleumier (1971: 193)

Rhytipterna – transferred from the Cotingidae, Snow (1973: 8); Ames (1971: 155)

Snethlagaea = *Idioptilon*, Fitzpatrick (1976) = *Hemitriccus*, here synonymized

Spizitornis 1920 = *Anairetes* 1850, Peters and Griswold (1943: 316)

Tolmarchus = *Tyrannus*, Meise (1949: 73); Bond (1958)

Tyranniscus (*nigrocapillus*, *uropygialis*, *cinereiceps*) = *Phyllomyias*, here synonymized; the remaining species are in the new genus *Zimmerius*.

Tyrannus – includes *Muscivora* and *Tolmarchus*, which see

Uromyias = *Anairetes*, Smith (1971: 275)

Xanthomyias = *Phyllomyias*, here synonymized

Xenopsaris – here placed at end of Tyrannidae, *incertae sedis*

Xenotriccus Dwight and Griscom 1927, Amer. Mus. Novit. No. 254: 1 – includes *Aechmolophus*, Webster (1968: 289)

Xolmis – includes *Pyrope*, Smith and Vuilleumier (1971: 193)

Yanacea – Carriker, 1933, Proc. Acad. Nat. Sci. Philadelphia **85:** 27 = *Anairetes*, here synonymized

Yetapa = *Alectrurus*, Short (1975: 269)

Zimmerius – here described, includes *Tyranniscus bolivianus*, *vilissimus*, *cinereicapilla*, *gracilipes*, and *viridiflavus* of Hellmayr

APPENDIX C

Ames' (1971: 158–162) Groups of Genera

1. *Fluvicola* group. The nucleus of this group is composed of *Xolmis*, *Neoxolmis*, *Agriornis*, *Muscisaxicola*, *Fluvicola*, *Gubernetes*, *Knipolegus*, *Muscipipra* and *Phaeotriccus*. *Hymenops* is probably an offshoot. *Satrapa* and *Entotriccus* probably also belong here. *Lessonia* agrees with them in musculature.
2. *Tyrannus* group. The group includes *Tyrannus*, *Muscivora*, *Tolmarchus*, *Tyrannopsis*, *Empidonomus*, *Myiodynastes*, *Megarhynchus*, *Conopias* and *Pitangus* (*sulphuratus* only).
3. *Nuttallornis* group. Closest to the *Fluvicola* group. Includes *Nuttallornis*, *Sayornis*, *Contopus*, *Blacicus*, *Empidonax*, *Aechmolophus*, *Aphanotriccus* and possibly *Muscigralla*.
4. *Myiobius* group. Includes *Myiobius*, *Terenotriccus*, *Pyrrhomyias* and *Onychorhynchus*. The manakin *Piprites* probably also belongs here.
5. *Myiarchus* group. Includes *Myiarchus*, *Eribates*, *Attila*, *Casiornis*, *Laniocera* and *Rhytipterna*.
6. *Colopteryx* group. Contains *Colopteryx*, *Oncostoma*, *Euscarthmornis*, *Hemitriccus*, *Myiornis* and *Lophotriccus*. *Platyrinchus* might belong near here. *Tolmomyias*, *Rhynchocyclus* and *Platyrinchus* differ greatly among themselves.
7. *Elaenia* group. Included are *Elaenia* (including *Myiopagis*), *Suiriri*, *Camptostoma*, *Tyrannulus* and *Phaeomyias*. *Microtriccus* and *Tyranniscus nigrocapillus* probably belong near here.

APPENDIX D

Figures 2 and 3, and Table II of Warter, 1965: 27–34

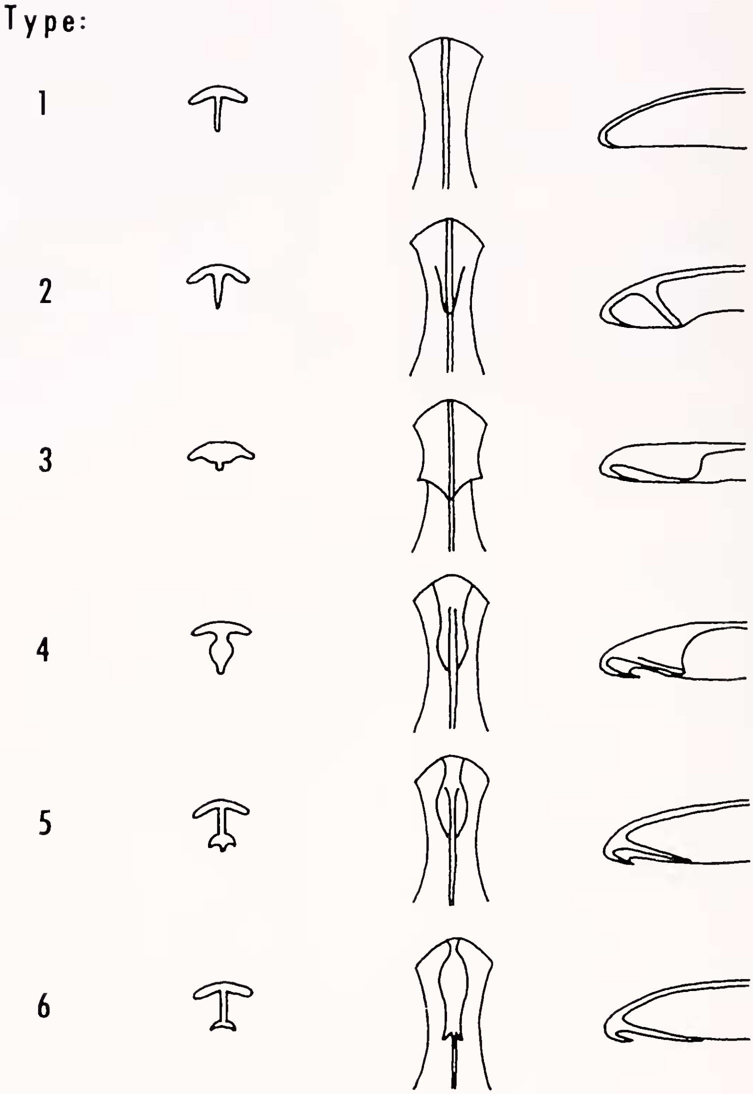

Figure 2. Types of Nasal Septa. Left column, cross section; center column, ventral aspect; right column, lateral aspect (all illustrations diagrammatic).

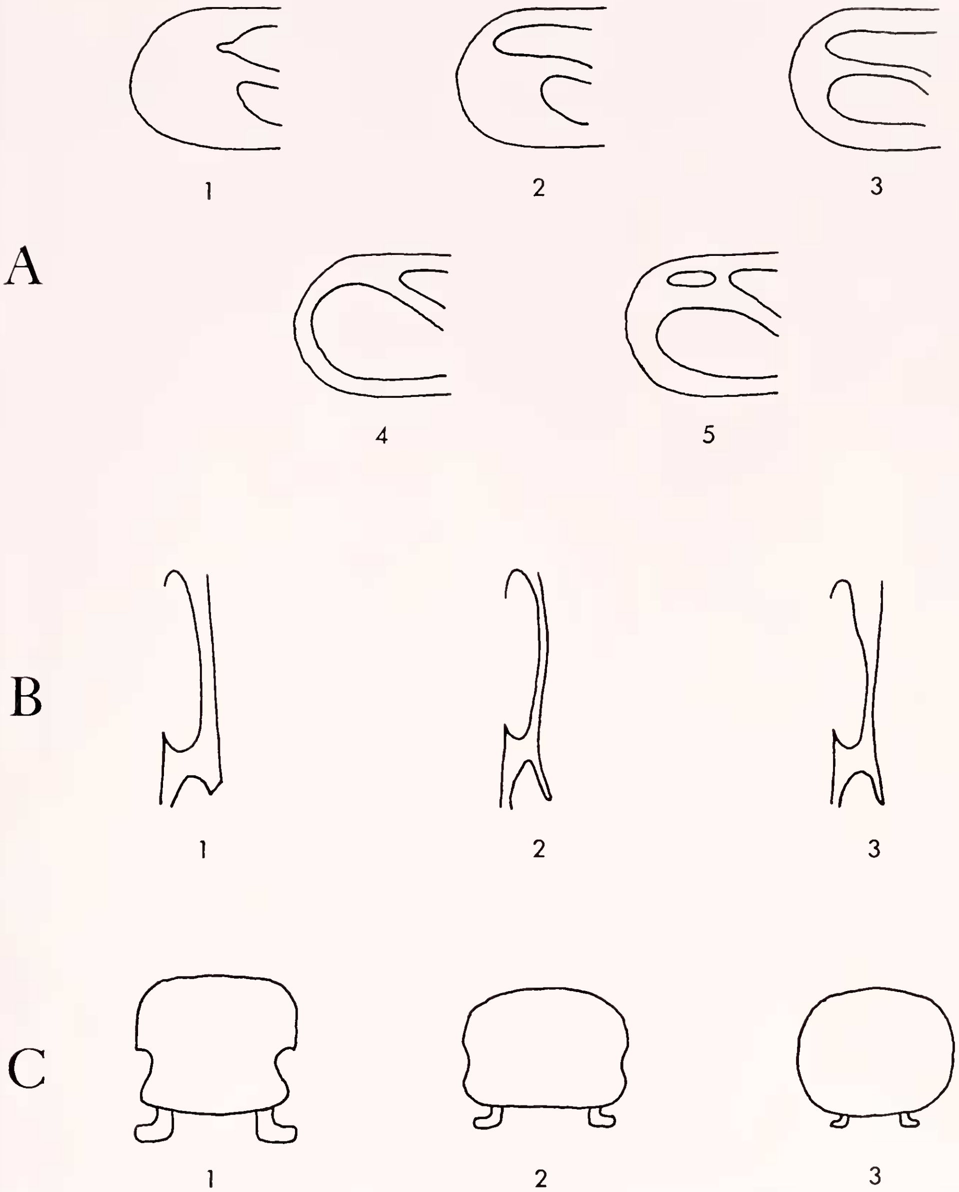

Figure 3. Features of Type I Skulls. A, types of interorbital septa; B, types of palatines; C, types of crania (posterior aspect).

TABLE 2. VARIABLE CHARACTERS OF FLYCATCHER SKULLS. NUMBERS IN COLUMNS REFER TO "TYPES" ILLUSTRATED IN FIGURES 2 AND 3. COLUMN I—NASAL SEPTUM. COLUMN II—INTERORBITAL SEPTUM. COLUMN III—PALATINES. COLUMN IV—CRANIUM. COLUMN V—PALATOMAXILLARIES (+ = PRESENT).

Genus	I	II	III	IV	V
FLUVICOLINAE					
Agriornis	6	2	1	1	+
Xolmis	6	2	1	1	+
Muscisaxicola	6	2	1	2	+
Lessonia	6	3	2	3	+
Myiotheretes	6	?	1	1	+
Neoxolmis	6	2	1	1	+
Ochthoeca	6	2	2	2	
Sayornis	6	2	3	2	+
Colonia	6	1(4)	2	2	
Gubernetes	6	1	1	1	
Yetapa	6	1(4)	1	2	+
Knipolegus	6	2	1	2	
Entotriccus	6	2	2	2	
Lichenops	6	3	2	2	+
Fluvicola	6	3	2	2	
Arundinicola	6	3	1	2	
Pyrocephalus	6	2	2(3?)	2	+
Ochthornis	6	2	1	2	
Muscigralla	5	2	1	2	
Satrapa	6	3	2	2	
Machetornis	6	2	2	2	
TYRANNINAE					
Muscivora	1	1	1	1	+
Tyrannus	1	1	1	1	+
Empidonomus	1	1	1	1	+
Legatus	2	1	1	1	
Sirystes	2	1	1	1	+
Myiodynastes	1	1	1	1	
Megarynchus	1	1	1	1	+
Coryphotriccus	1	1	1	1	+
Myiozetetes	1	1	1	1	+
Tyrannopsis	1	1	1	1	+
Pitangus	1	1	1	1	+
Tolmarchus	1	1	1	1	+
MYIARCHINAE					
Myiarchus	2	1	1	1	+
Rhytipterna	2	1	1	1	+
Eribates	2	1	1	1	+
Nesotriccus	2	4?	1	3	
Nuttallornis	6	1	2	1	
Contopus	6	1	3	2	+
Blacicus	6	1	3	2	
Empidonax	6	2	3	3	+
Aechmolophus	6	2	3(2)	2	
Cnemotriccus	6	2	2	2	
Mitrephanes	6	2	3	2	
Terenotriccus	6?	2	3	3	
Myiobius	6	1	3	2	
Pyrrhomyias	6	4?(1)	3	2	
Myiophobus	6	4?(1)	2	2	
Onychorhynchus	3	1	3	1	+
PLATYRINCHINAE					
Platyrinchus	3	4	3	3	
Cnipodectes	1(3)	4	1(2)	2	+
Tolmomyias	1(3)	4	1	2	
Rhynchocyclus	1(3)	4	2(3)	2	
EUSCARTHMINAE					
Todirostrum	2	4	2	3	
Oncostoma	1	4	1	3	
Euscarthmornis	1?	4	1(2)	3	
Snethlagaea	1	4	2	3	
Lophotriccus	2	4	2	3	+
Colopteryx	?	4	2	3	+
Myiornis	1	4	2	3	+
Pogonotriccus	3?	4	2	3	
Leptotriccus	?	4	2	3	
Phylloscartes	1	4	2	3	
Capsiempis	2?	4	2	?	+
Pseudocolopteryx	2?	4	1(2)	3	
Habrura	6	3	2(1)	3	
SERPOPHAGINAE					
Tachuris	?	4	2	3	
Spizitornis	5	4	2	3	
Stigmatura	2	4	2	3	
Serpophaga	5	4	2	3	
Inezia	5	4(3)	2(1)	2	+
Mecocerculus	5	4	1(2)	3	
ELAENIINAE					
Myiopagis	1?	3	1	3(2)	
Elaenia	5	1	1	2	+
Suiriri	5	2	2	2	
Sublegatus	5	1	2	3	
Phaeomyias	2	2	2	3	
Camptostoma	2	4	2	3	
Xanthomyias	1	4	?	3(2)	
Tyranniscus	6	3	2	3	+
Tyrannulus	2	3	?	3	
Microtriccus	2–3	4	1	3	
Leptopogon	3	4	1	2	+
Mionectes	5?	4	1	2	+
Pipromorpha	5?	4	?	2	+

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